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A MICROSCOPIC STUDY OF CONIFEROUS WOOD IN RELATION TO ITS STRENGTH PROPERTIES[1]

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I. Introduction

In a broad sense this study is motivated by a desire to add to the meager knowledge of the role played by the individual cells in the resistance of the wood to mechanical forces. More specifically, the problem is concerned with the identification of wood which is abnormally low in strength. Since it is recognized that woods of greater density are the stronger, an abnormal-strength specimen is one that is weaker than the average for the density range in which it occurs.

Research on the strength properties of wood has been quite empirical, and the data given have represented large numbers of specimens either as average values or as average trends of relationships. Winslow ('33), in outlining the state of research in forest products, has this to say of the mechanical properties of wood:

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[1] An investigation carried out in the Graduate Laboratories of the Henry Shaw School of Botany and the Department of Civil Engineering of Washington University and submitted as a thesis in partial fulfillment of the requirements for the degree of doctor of philosophy in the Henry Shaw School of Botany of Washington University.

[2] A fellowship established by the American Creosoting Co.

> The information we possess as to strength properties has been collected with only incidental reference to structure; the direction (longitudinal, radial, or tangential) in which the force was applied was commonly known, and one structural characteristic, density, was always determined. The finer details of structure were not determined, however, nor were the tests designed to show the effect of structural variations in any minute degree.

Thus there is no considerable body of literature bearing directly upon the cellular variations related to strength. One type of clear coniferous wood of abnormal-strength properties has been known for over forty years, but until recently its description has been vague. Whether this is the only type of abnormality is not known, nor is it known whether the factors causing this abnormality are also responsible for what might be called the normal variation of strength in relation to density.

The purpose of this study is not the investigation of any given type of structural variation, but the investigation with the microscope of the differences between strong and weak specimens of a wood of simple anatomy that have been subjected to simple stresses. Further, an interpretation of the microscopic data is attempted against a background of the literature pertaining to factors known to affect the strength of wood.

II. Review of the Factors Affecting the Strength of Wood

Although the experimental part of this problem is only intended to constitute a step in the direction of complete control of the factors affecting strength of wood, a review of what is known of these factors is necessary for a full understanding of the problem, the methods used, and for an interpretation of the results. The discussion will be concerned with coniferous wood except where work on other wood applies, and the characteristics of southern pine will be emphasized.

Because it is at present the only generally known type of clear coniferous wood of abnormal-strength properties, "compression wood" will be frequently referred to in this paper. The term is synonymous with the German expressions "Rotholz" and "Druckholz." Büsgen and Münch ('29) gave a

good account of its causes and occurrence, and Trendelenburg ('32) and Pillow and Luxford ('37) have recently reviewed its technical properties. The literature will not be reviewed here, but it is of interest to note that Roth ('95) recognized the structure in the trunks of southern pine, but seems to have been ignorant of the properties of the wood. There has been some confusion in the descriptions of "compression wood," so that it would be well to quote from the summary of the most recent and the most comprehensive paper on the subject, that by Pillow and Luxford ('37):

> Under a microscope the summerwood tracheids of compression wood appear to be nearly circular in cross section whereas those of normal wood are more or less rectangular. The fibrils of the secondary cell walls in compression wood make a higher angle in relation to the longest axis of the cells than do the fibrils in normal wood and these walls contain microscopic checks.
>
> The lignin content of compression wood as indicated by the species investigated is slightly higher and the cellulose content slightly lower than normal wood. The weight of pronounced compression wood is from 15 to 40 per cent greater than normal wood. The longitudinal shrinkage of compression wood from the green to oven-dry condition varies from about 0.3 to 2.5 percent whereas normal wood has a shrinkage from about 0.1 to 0.2 percent. The transverse shrinkage of compression wood is less than that of normal wood.
>
> When adjustments are made for differences in weight, compression wood is lower in practically all strength properties as compared to normal wood. . . . The increase in strength properties accompanying drying of the wood is not so great for compression wood as for normal wood. Compression wood is under compression in the log and when the stresses are released, such as by sawing, extension of the compression wood portion occurs.

There is still much to be known about this type of wood, but until a more descriptive term can be applied, it must be referred to by its accepted English designation, "compression wood." It will be used in this paper with quotation marks to avoid associating it with the compression strength properties.

There may also be reference to the German terms "Weissholz" and "Zugholz" (tension wood) which have been applied to the wood diametrically opposite in the stem to "Rotholz."

DENSITY

The two factors controlling density of wood are the density of wood substance (cell-wall material) and the porosity or proportion of air space to cell-wall volume. The apparent

density of wood substance seems to be one of the most invariable features of wood. Hartig ('85) was satisfied to use the single value 1.56 for several species of conifers. Dunlap ('14) found a range of 4.5 per cent in seven species including hardwoods and softwoods, but only insignificant variation between two determinations of the same species. He found 1.506 gr. per cc. for longleaf pine by floating thin sections in a calibrated solution of calcium nitrate. Stamm ('29) made a study of the density of wood substance and came to the conclusion that it "varies slightly among species as a result of variation in the chemical composition of the substance." He obtained densities of 1.598 for cotton cellulose, 1.594 for isolated Cross and Bevan wood cellulose (from catalpa heartwood), 1.451 for isolated lignin (insoluble in 72 per cent H_2SO_4, from western yellow pine heartwood), and 1.531 for loblolly pine wood substance. All these data were from the same method, water displacement at 25° C. Berkley ('34), using a pycnometer method on sawdust, found a range of 1.5156 to 1.5273 gr. per cc. embracing three species of southern pine.[1] It seems evident that variation in cell-wall density has little to contribute to the wide variation observed in the strength of woods of the same specific gravity. Also it appears justifiable to use the specific gravity of wood as a criterion of the relative amount of wood substance in a specimen, at least in a series from the same kind of wood.

The real basis, then, for the strength-specific gravity correlation which is known for wood is the relative amount of solid substance under the stress. The deviations from the strength-specific gravity regression must be due to some property of the solid material, either its arrangement (size, shape, and distribution of the cells) or its internal structure and constitution.

The great bulk of coniferous wood is made up of fibers the length of which is about 100 times the breadth. The end walls

[1] The term "southern pine" refers to the hard or yellow pines native to southeastern United States, the most common species of which are longleaf pine, *Pinus palustris* Mill., shortleaf pine, *P. echinata* Mill., and loblolly pine, *P. Taeda* L. These woods are not distinguishable anatomically though there are statistical differences in specific gravity and growth-ring measurements. The last two are frequently designated together as "commercial shortleaf pine."

are tapered to points so that all but an insignificant amount of the solid material occurs as vertical tube walls. A cross-section of these tubes, then, presents an approximate map of the volumetric proportion of solid to air space, and the ratio *cell-wall area ÷ wood-section area* may be regarded as equal to the ratio *specific gravity of wood ÷ specific gravity of wood substance:*

$$\frac{\text{cm.}^2(\text{sub.})}{\text{cm.}^2(\text{wood})} = \frac{\text{cm.}^3(\text{sub.})}{\text{cm.}^3(\text{wood})} = \frac{\text{gr./cm.}^3(\text{wood})}{\text{gr./cm.}^3(\text{sub.})}$$

When a stress is applied to a cross-section of a wood specimen (stress parallel to the fibers), it can be referred to the solid material by multiplying it by the ratio, *sp. gr. substance ÷ sp. gr. wood:*

$$\text{kg./cm.}^2(\text{sub.}) = \text{kg./cm.}^2(\text{wood}) \times \frac{\text{gr./cm.}^3(\text{sub.})}{\text{gr./cm.}^3(\text{wood})}$$

And, since sp. gr. of wood substance may be considered as constant, an index of the strength of the wood substance may be had in the quotient, *strength of wood ÷ sp. gr. of wood.*

In studies of the strength of wood different methods of eliminating specific gravity have been used by various workers under different designations. Botanists investigating the mechanical systems of plants (Schellenberg, '96, Sonntag, '03, Ursprung, '06) referred stress to the cell walls by making camera-lucida drawings of the cross-sections of the specimens, and measuring the areas of the walls and the lumens to obtain the ratio of substance to wood.

Kollmann ('36) reports the use by Monnin in 1919 of a quality index for judging wood for airplane construction:

$$\text{“Statische Kennzahl, } I_s = \frac{\sigma_{-B}}{100 \cdot r_{15}}\text{”}$$

where σ_{-B} is the compression strength in kg./cm.^{2}, r_{15} is the specific gravity of the wood at 15 per cent moisture content in

gr./cm.[3], and I_s is the index in kilometers. Kollmann also compared wood with other materials in tensile strength by the factor "Reisslange" (breaking length), *tensile strength ÷ specific gravity.* He attributed this term to von Reuleau in 1861, who evidently used it as a measure of the strength of wires and threads. It represents the length a strand can attain without breaking under its own weight in tension, all the terms being in the metric system. Rothe ('30) converted his strength data to those of strength of cell-wall substance by multiplying the compression stress by the ratio *sp. gr. wood substance ÷ sp. gr. wood,* and gave essentially the same justification given above. Trendelenburg ('31) compared European and American Douglas fir by the quotient, *strength ÷ sp. gr.* Lassila ('31) and Jalava ('34) used the same fraction, calling it the "Janka quotient," in comparing pine from different forest types in compression strength. Markwardt and Wilson ('35) used the same quotient to compare compression strength of a very light species and a very heavy one and called it "Specific Strength." In relating strength to cell-wall structure Pillow and Luxford ('37) used as the dependent variable the "ratio of strength to specific gravity," in which the specific gravity was raised to a power expressing its empirical relationship to the particular strength property involved. The curvilinear strength-density correlation provided here takes the regression line through the zero-zero origin, but in the range of the concentration of data the exponents used give very nearly a straight line, so that this ratio is not incompatible with the stress-density theory given above.

Berkley ('34) tended toward eliminating specific gravity in his study of strength properties by choosing for analysis the specimens deviating most from the regression of strength over specific gravity. Clarke ('36) employed the same method when he compared "outlying" specimens in the same specific gravity range.

GROSS STRUCTURE

It is generally known that strong wood in conifers is associated with an optimum growth ring width for each kind of wood

and with a high percentage of summerwood. Thus Wilson ('34), speaking of the quality of wood for structural timbers, states:

> Selection for rate of growth requires the number of annual rings per inch on the end of the piece to be within a specified range. Selection for density imposes in addition to the limitations of growth the requirement of a minimum percentage of summer wood.

Structural grading rules for coniferous woods generally follow these principles.

(a) Growth Ring Width.—This is commonly regarded as only indirectly affecting strength through specific gravity. The optimum ring width for strength appears to be the optimum for specific gravity. Thus, Markwardt and Wilson ('35) illustrate the effect of rate of growth in conifers with a graphical correlation of specific gravity over rate of growth, showing optima for different stand types of redwood near twenty rings per inch. Trendelenburg ('31) shows that specific gravity and strength have the same optimum ring width for Douglas fir. Paul ('30) further connects growth rate with specific gravity and with percentage of summerwood:

> Both very wide and very narrow annual rings in conifers usually contain a larger proportion of the spring-wood layer, so that in these species wood representing either extreme of growth may be low in specific gravity.

Alexander ('35) has given for Douglas fir average figures and graphical correlations of compression strength and specific gravity over rings per inch on the same chart with superimposed ordinates. The straight-line curves for the dependent variables are both somewhat irregular but they have nearly the same irregularities. This seems to substantiate the assumption that specific gravity is the controlling factor here (fig. 1). The present writer has plotted Alexander's average data as strength per unit density over rings per inch in fig. 2, the new data representing the average crushing strength divided by the average specific gravity for each rings-per-inch class. The result seems to indicate that only part of the relation between ring width and strength is due to specific gravity and that some other factor affecting strength varies fairly regu-

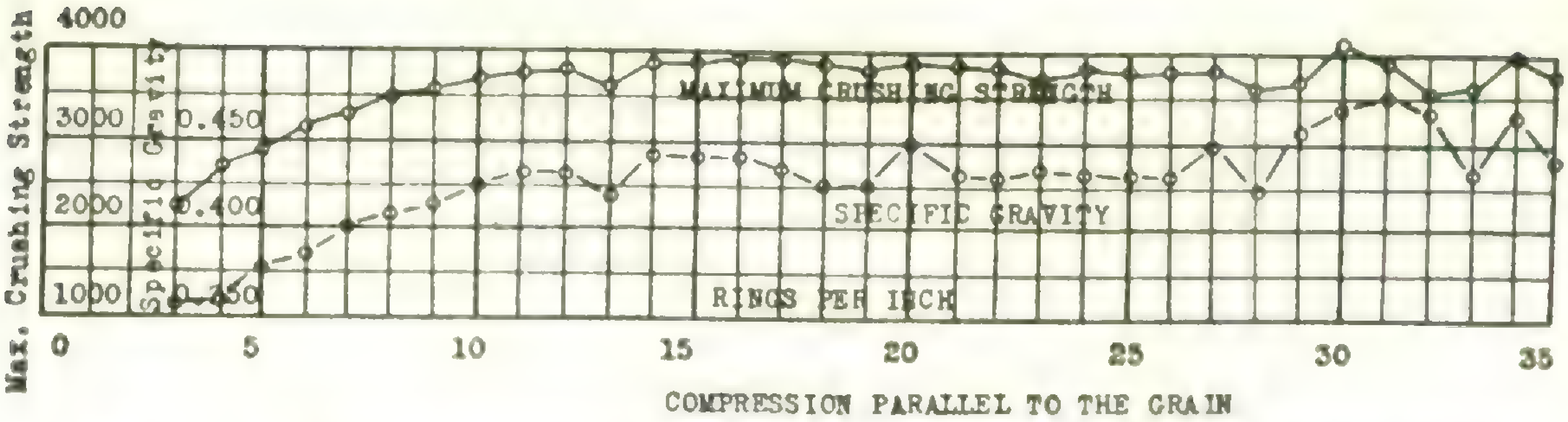

Fig. 1. Average compression strength parallel to the grain and average specific gravity plotted over rings per inch for green Douglas fir. (After Alexander, '35.)

larly with growth rate. Since the original material was chosen to be truly representative of "every varying condition of structure from pith to bark and from stump to top," the low strength on the rapid-growth end of the curve is probably partly due to the presence of wide-ringed material such as "compression wood" and wood near the pith, which are known to be abnormal in strength properties.

Koehler ('38) indicates that wide-ringed loblolly pine ranks low in most strength properties for its specific gravity and has certain resemblances to "compression wood." He shows graphically the high frequency of wood of high longitudinal

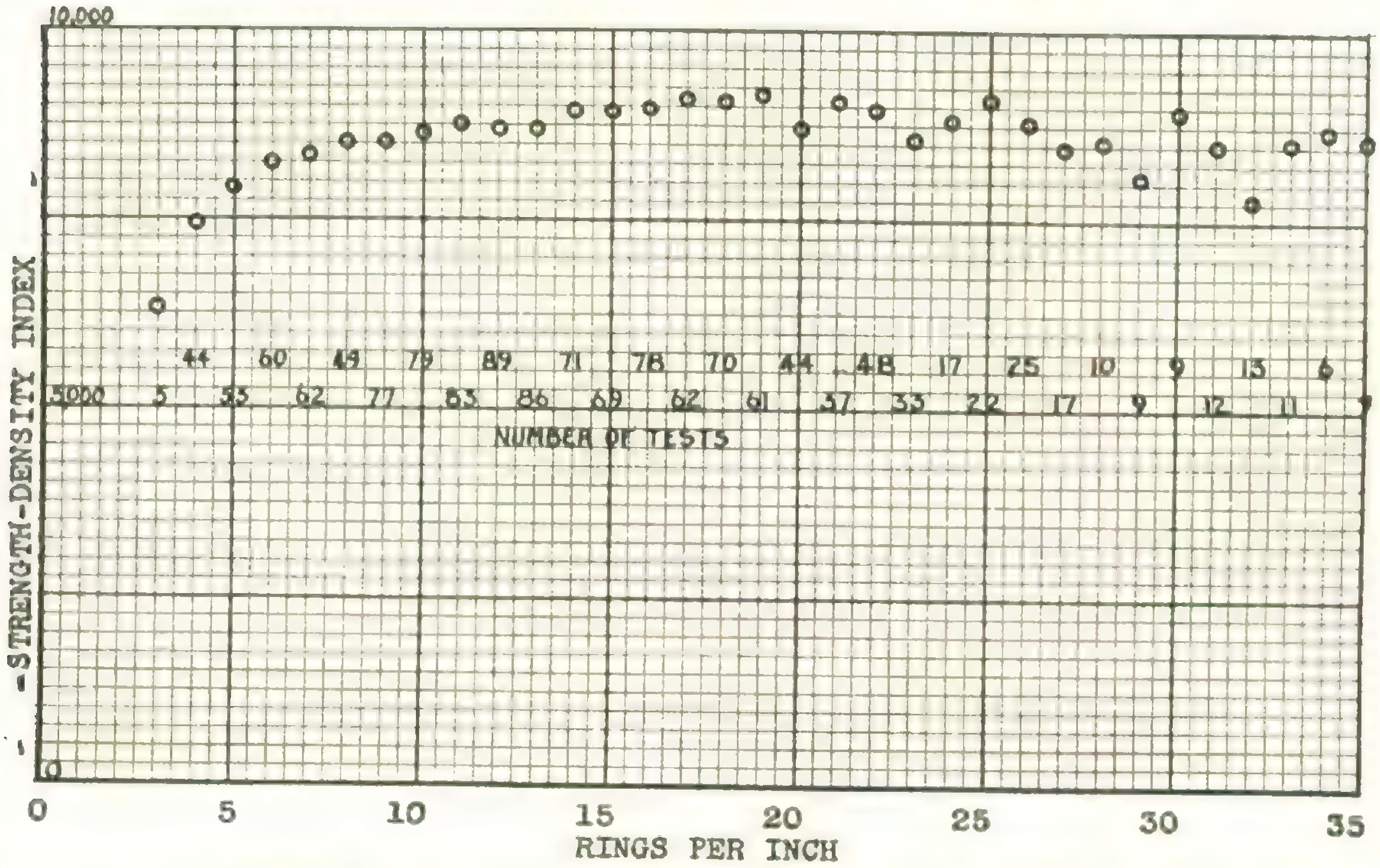

Fig. 2. Strength-density index (average compressive strength in lbs./in.² ÷ average specific gravity in gr./cc.) plotted over rings per inch for the data of fig. 1.

shrinkage among wider-ringed specimens of loblolly and slash pine. This feature is typical of "compression wood."

(b) Percentage of Summerwood.—The visual estimation of density of coniferous wood is based on the fact that summerwood is more dense than springwood. Percentage of summerwood is a good criterion of specific gravity only in so far as its density is constant. Grading rules control this factor only in specifying that the color of the summerwood be dark. It is certain that there are variations in density of summerwood within any species and that the relative areas of springwood and summerwood cannot be used as true criteria of mechanical properties unless they are qualified by specific gravity. With wood density and percentage of summerwood constant, the distribution of solid wood substance between springwood and summerwood may vary. This would reflect variations in fiber measurements (cell diameter and wall thickness) which perhaps affect the strength properties of the individual cells. At least, we can conceive that two tubes of the same material, length, and cross-sectional wall area, but with different diameters and wall thicknesses, would react differently in end compression. Clarke ('33) made a correlation study of strength, specific gravity, ring width, and percentage of summerwood in ash. Since with specific gravity constant, strength decreased with an increase of summerwood, he concluded that the thickness of the walls of the summerwood fibers is an important controlling factor.

The empirical nature of the previous research on the mechanical properties of wood is attested by the dearth of literature on the strength of isolated springwood and summerwood. In the first part of the century botanists considered this aspect, but they worked with what is regarded as abnormal wood and the methods of testing were not well controlled. Sonntag ('03) reported on the tensile strength of spruce specimens of 1 mm.-square section in "Rothholz" ("compression wood") and "Weissholz" (white wood, wood diametrically opposite "compression wood" in the stem). Although his tests were few and widely varying, summerwood was found to be stronger than

springwood in tension parallel to the fibers in both types of wood, even basing the stress on cell-wall area. Ursprung ('06) reported the same relation for springwood and summerwood of the upper and lower sides of branches of spruce in both tensile and compressive strength. Von Schrenk ('28), testing small beams of southern pine, found that springwood had roughly half the maximum fiber stress of summerwood. Forsaith ('33) used small beams (2″ × .09″ × .09″), each with a single layer of springwood and one of summerwood. He reported bending strength and stiffness when these layers were in different positions (springwood up, springwood down, and springwood at side.) He concluded that summerwood is stronger in compression than springwood is in tension, and that "the difference between the ultimate strength in tension and compression is greater in springwood than in summerwood," also, that "stiffness is more or less controlled by the summerwood."

It may be concluded that there is a need for a study of growth rate and strength-density which carries the controls down to measurements of cell diameters and cell-wall thicknesses in springwood and summerwood of carefully chosen normal wood.

(c) Heartwood and Sapwood.—In the wide testing experience of the Forest Products Laboratory (Markwardt and Wilson, '35) "no effect on the mechanical properties of most species due to change from sapwood to heartwood has been found." The structural features do not change in the process, but the heartwood is infiltrated with added materials which may be dissolved out with apparently no effect upon the wood substance. Luxford's ('31) tests on species high in heartwood extractives indicate that heartwood has some strength advantage, especially in compressive strength parallel to the grain.

Where specific gravity is to be rigidly controlled it should be remembered that extractives add to the weight of heartwood, and this may be considerable in resinous species. Berkley ('34) was able to improve his relationships of strength over specific

gravity for southern pine by correcting specific gravity for benzol extractive.

HISTOLOGY

Differences in the kinds of cells, their proportions and their arrangements, may be expected to explain partially differences in strength properties among woods of different anatomical types. Likewise, variations in amounts of different cellular elements might cause variations in the strength-density relationship of a group of specimens of the same anatomy. In elucidating the causes for brashness in wood Koehler ('33) gave deficiency of wood fibers[1] (oak) as one of the reasons for deviations in the relation of per cent of summerwood to toughness. In this case there would be an excess of wood parenchyma, a cell type that differs from the wood fiber not only in the relation of wall thickness to cell diameter but also in morphology.

Coniferous woods are simple in that the vertical elements are of only two general kinds, parenchyma cells and tracheids, and the latter predominate. In the pines, wood parenchyma is normally confined to one or two layers of thin-walled flattened cells surrounding resin canals. Vertical resin canals are intercellular spaces without walls, and so do not affect the strength of wood substance except as they account for the presence of parenchyma. Their effect on the strength of wood is limited to an interruption of the solidity of the tracheid mass. Berkley ('34) found the diameter of resin ducts in southern pine varying from 0.19 mm. to 0.25 mm. The cross-sectional area was 0.66–2.5 per cent, and the variation between strong and weak specimens was evidently not significant.

Wood rays certainly must play an important role in the distribution of stresses in wood, but there is little definitely known about this. They exclude part of the weight of the wood from participating in efficient axial stress resistance and they cause deformation of the contours of adjacent tracheids. On the other hand, they form a very effective lateral bracing and

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[1] The term "wood fiber" refers to a particular type of cell found in hardwoods. The term "fiber" when used alone refers to fibrous cells in general.

seem to make up for the weaknesses that might be due to a lamellar (springwood and summerwood) structure. In end compression tests, wood fractures quite regularly in a sloping radial plane. Berkley ('34) attributed this directly to the rays and reported that Thil in 1900 and Fulton in 1912 agreed with him. Jaccard ('10), Robinson ('20), Forsaith ('33), and Bienfait ('26) each observed that initial failure is not associated with the rays. Iwanoff ('33) found that the fibers bend most frequently at the rays, but that there is another more angular type of fiber failure that is not dependent upon the rays. Bienfait ('26) saw no difference between radial and tangential walls as to indications of initial compression failure. He suggested that the plane of fracture is indirectly caused by the stiffening effect of the wood rays against gross fracture in a tangential plane. Koehler ('33) regards the rays as ineffective in determining resistance to toughness. Among Berkley's ('34) outlying specimens of southern pine, in the graphical correlation of compressive strength with specific gravity, the weaker specimens averaged about one per cent more of total area occupied by resin ducts and wood rays than the stronger specimens. He concluded that the larger number of wood rays and resin canals contributed to the weakness of the material, especially the wide-ringed, short-fibered wood in the first few rings near the pith.

Fusiform rays (containing horizontal resin canals), also measured by Berkley, varied from 0.053 to 0.075 mm. in width and from 0.35 per cent to 1.61 per cent of total area. He regarded them as effective in causing compression failures.

It seems reasonable that the rays may play two opposing roles in the resistance to stress in wood, which may be partially compensating.

TRACHEID MORPHOLOGY

Forsaith ('26) stated that tracheids occupy 90 per cent of the stelar volume in conifers. Berkley ('34) showed that resin ducts and rays occupy roughly 10 per cent of the cross-sectional area in southern pine. Since the ray and parenchyma cells have much thinner walls than tracheids, it is certain that tracheids

constitute well over 90 per cent of the weight of this type of wood. It would seem that an explanation of the large strength-density variations must be associated with this element.

The tracheid is defined as an "imperforate cell with pits to congeneric elements bordered" (Record *et al.,* '33). In southern pine its length is about 100 times its greatest breadth. It varies in cross-section from approximately isodiametric, large-lumened, thin-walled in springwood, to tangentially flattened, small-lumened, thick-walled in summerwood. Normally these cells fit closely together in well-defined radial rows. The cells of "compression wood" are more or less rounded in cross-section, have larger lumens in summerwood and thicker walls in springwood than normal wood, are less regular in arrangement, and may have intercellular spaces among them at the corners. The walls of normal tracheids are parallel except near the ends where they taper to a point in summerwood or to a radially oriented wedge in springwood. The ends may be more or less curved radially. Abnormal cells may have irregular curvature throughout the length, which, according to Berkley ('34), is associated with specimens weak in end compression.

The length of tracheids varies considerably among specimens of the same wood. Short tracheids are known to be associated with "compression wood" and the wide-ringed material of the first several years' growth. Berkley ('34) found the average length of tracheids in his southern pine specimens to be between about 2.5 mm. and 5.0 mm. However, the average length of tracheids for his strongest and weakest woods was about the same. Koehler ('33) saw no relation between tracheid length and toughness and attributed this to the fact that the fibers are cemented firmly together and a slipping between fibers is not involved in failure. Sonntag ('03) found considerable difference in the range of tracheid length between "compression wood" and "tension wood" but did not attribute the low tensile strength of "compression wood" to this. Since stresses parallel to the fibers actually cause failure in diagonal shear and since the contour of the fiber is not uni-

form throughout its length, it is probable that the above conclusions are valid in spite of the fact that some types of weak wood have short fibers.

Bordered pits are confined to the radial walls of tracheids almost exclusively. A bordered pit is defined as "typically, a pit in which the cavity becomes abruptly constricted during the thickening of the secondary wall" (Record *et al.*, '33). Viewing an isolated tracheid the bordered pit appears as a saucer-shaped depression on the wall with a small circular opening at its center, the canal. The pits of contiguous tracheids are paired so that the depressions form a lenticular space, the chamber. In springwood the whole wall takes the form of the chamber and has about the same thickness throughout except for a rounding off at the canal. In springwood of southern pines the chamber (marking the border) extends to half or more the width of the cell. In summerwood the border and canal are smaller, the chamber is shallower in the wall surface, and the canal extends from the outer aperture (at the chamber) to the inner aperture at the inner wall surface. Usually the inner aperture is more or less lens- or slit-shaped. Bordered pits are much less numerous in summerwood than in springwood.

Jaccard ('10) and Tiemann ('06) regarded the bordered pits as points of weakness in compression, but Robinson ('20), Bienfait ('26), and Forsaith ('33) did not agree. Forsaith observed that both compression and tension failures avoid the pits and that the line of fracture runs around the border rather than through the canal. Koehler ('33) regarded bordered pits as stronger than other parts of the wall because of concentric fibrillar arrangement in the overhanging wall. Sonntag ('03) found larger bordered pits and especially longer pit slits in "compression wood" than in "tension wood" of spruce branches and assigned this as a cause for lower tensile strength of "compression wood."

Each conifer tracheid comes in contact with a wood ray at a number of places in its length. At these crossings the tracheid wall is indented or the whole cell is bent to conform

to the lenticular cross-section of the rays. This bending of the fiber wall has been blamed for a lower resistance of the wood to axial compression stress. In the ray crossings the pits to the ray parenchyma cells have large canals, and the reduction in wall section may be considerable. Forsaith ('33) observed that the line of fracture (tension?) may shift slightly to take advantage of these pits.

It has been shown that there are several features of the architecture of the individual tracheid the variation of which may have an effect on the strength of wood as a whole. The study of the parts played by these features is complicated by the fact that the fibers are cemented together with a material which seems to hinder the fibers from acting individually. Thus from his microscopic examination of fractures in small bending specimens, Forsaith ('33) concluded that:

> . . . the plane of fracture follows the area of maximum stress, and that anatomical inequalities in wood do not deflect the line of cleavage more than a few microns. Furthermore, where fracture does jump from cell to cell, there seems to be no specific reason why it should depart from the middle lamella line at this point. All things considered, it would appear that the minute structure of the wood plays a relatively unimportant part in locating failure, in comparison with that determined by a concentration of stresses in the region of maximum moment.

This may be valid for bending fractures because here the longitudinal stresses are concentrated under the loading point. And especially is it true for Forsaith's tests where one kind of stress was confined to one part of the annual ring and there was not the complication of stresses as in the whole wood where two different kinds of material are involved.

The axial compression test, too, seems to be ill adapted to the study of centers of weakness in the cell structure. Once failure takes place in a relatively small group of cells, or theoretically at a certain point on the wall of a single cell, the fracture seems to affect the neighboring cells and the progress of the effect often proceeds in a quite regular pattern without much selection of points of weakness. In axial tension fracture, however, there is little regularity, and it seems valid to assume that the pattern of fracture is determined by the points of

weakness in the individual fibers which may be associated with contour features.

TRACHEID WALL STRUCTURE

With ordinary microscopic methods fiber walls of light-colored woods (and sapwood) usually appear quite transparent and without structure. With staining, a thin outer layer may be differentiated, and under certain conditions striations and checks may be seen in longitudinal view which indicate a spiral structure. Polarized light confirms the concentric and helical anisotropy. Chemical or mechanical micro-dissection may serve to separate fine threads or fibrils from the wall. These facts have been known for nearly a century, but only recently have details been provided for even the structure of the cell wall within the range of the microscope. Below microscopic range an hypothetical crystal-like unit suggested by Nägeli in the middle of the last century, and named by him the "micelle," has been widely accepted. Since then the concept has been carried over into the field of colloidal chemistry where the unit is often designated as one type of crystallite. Although great advancement has been made in the understanding of the sub-fibrillar structure of the plant cell wall since Nägeli's time, the micelle is still without exact definition.

The recent work by I. W. Bailey and his associates on the cambium and its derivative tissues has yielded the most lucid exposition yet available of the visible structure of the conifer tracheid. Kerr and Bailey ('34) gave the results of their optical and chemical differentiation of the lamellae of normal woody fibers and offered a terminology to clear up obvious discrepancies in designation by earlier workers. This terminology is used in the present paper. In order from the outermost layer the terms are: middle lamella (or intercellular substance), cambial (or primary) wall, and secondary wall with its outer, central and inner layers.

Between contiguous mature fibers is a single layer of optically anisotropic material known as the middle lamella. It is quite thin except between the rounded corners of the tracheids,

and is difficult to distinguish from the true primary wall layers of the two adjacent cells because all three are highly lignified. It has been shown to contain, besides lignin, substances which are dissolved by solvents for polyuronides.

The outermost true layer of the cell wall is designated the primary or cambial wall. This is the original wall of the cambial initial, and though very thin and highly lignified it has been shown to have retained a true cellulose structure and also some of the original polyuronides of the cambial initial. The cellulose in the primary wall is shown to have positive birefringence in both transverse and longitudinal sections. Bailey ('38) has observed a wide variety of structural patterns which are all porous but coherent. His figure suggests the "folienstruktur" of Frey-Wyssling ('35), who attributed it to all primary meristems. In this structure the cellulose is layered in the plane of the cell wall but is not oriented in a direction perpendicular to this plane. Because of its thinness and lack of orientation the primary wall may act mechanically with the true middle lamella as an amorphous substance, the binder between the cells.

Next within the primary wall lies the secondary wall. By its optical activity it is seen to consist largely of well-oriented cellulose, though it is usually more or less lignified (Bailey and Kerr, '35, '37), with the lignin constituent variously distributed. Normally in tracheids the secondary wall is divided into three consecutive layers according to the fibrillar orientations: (1) a thin layer (next to the primary wall) with the fibrillar orientation in a relatively flat helix (45° to almost 90° with the cell axis); (2) a thick central layer with fibrils in a relatively steep helix (almost 0° to 45° with the cell axis); and (3) a very thin inner layer with fibrils in a more or less flat helix. The inner layer is least well known though its anisotropy has been shown by birefringence in both longitudinal and transverse sections of the wall.

The fibrillar structure of the central layer may often be detected with ordinary microscopic methods. It is evident from striations and checks in the wall and from the threads or fibrils

of cellulose which can be dissected mechanically (Seifriz and Hock, '36, and others) and chemically (Ritter, '35, and others). The outer layer may also be seen to be made up of thread-like fibrils if it is viewed apart from the central layer. Although Ritter ('35) has shown fibrils to occur as threads as long as 230 μ, Bailey and Kerr ('35) maintain that the cellulose of the central layer occurs in a continuous system of heterogeneous elongated and anastomosing "complexes." They state:

> The form and size of the fragments which may be dissected from the secondary wall are clearly dependent upon the structural pattern of the matrix of cellulose and upon the type and severity of the chemical and mechanical treatments to which the material is subjected.

It is feasible to agree with them that the wide variety of proposed "ultimate units" of cellulose may be due to differences in chemical technique. Their concept of the fibrillar structure includes the interweaving of an anastomosing system of non-cellulosic materials within the interstices of the cellulose structure, and they have shown photographic evidence of similar patterns obtained by treatment with lignin solvents and with cellulose solvents. These chemical patterns will be discussed in the next section.

Bailey and Vestal ('37), with a method of forming iodine crystal aggregates within the interstices of the cellulose structure, have presented convincing evidence of the structural orientation in the outer and central layers of normal conifer tracheids. Their survey indicates that the angles of orientation are not specific for species of wood. They regard as the normal condition in summerwood an axial orientation of the central layer and a helical one for the outer layer; in springwood the central layer is helical and the outer layer is perpendicular to the axis. These patterns were not found to be strictly confined to each part of the annual ring. The angles of orientation may vary from cell to cell, so that combinations of axial central wall with transverse outer wall and helical central wall with helical outer wall were of common occurrence.

Regarding changes in orientation within the central layer, Bailey and Vestal ('37) state:

> The orientation of the fibrils may fluctuate, at times, in the successively formed growth rings[1] or lamellae of the central layer, but pronounced shifts are of relatively infrequent occurrence in the tracheids of conifers. Regularly recurring changes from right-handed to left-handed helixes or *vice-versa*, such as are hypothesized by various investigators, are rarely, if ever, encountered in the central layer of coniferous tracheids.

Scarth, Gibbs, and Spier ('29), Lüdtke ('31), and others have described the secondary wall of fibers as made up of as many as ten or more concentric laminae, the direction of the slope of the fibril axis alternating with each layer, and with these laminae constituting separate cellulose structural systems separated by layers of amorphous material. Ritter and Chidester ('28) gave photographs of elm fibers in which the sleeve-like lamellae have been made to telescope by chemical treatment, and they attributed this structure to wood fibers in general. Bailey and Kerr ('35) ascribed it to only certain types of cells. They concluded, after a wide survey of gymnosperms and angiosperms, that the secondary wall of normal tracheids, fiber-tracheids, and libriform fibers consists of but three layers of varying orientations (as indicated above), and further that the central layer consists of a continuous structural system (the cellulose matrix with an interwoven non-cellulosic structure).

The iodine-crystal technique of Bailey and Vestal ('37) has given detail in fibrillar deviations within a given wall layer. The linear fibrillar structure of the outer layer seems to be discontinuous at the border (chamber) of the bordered pits, and within the border the fibrils are in concentric orientation. The fibrils of the central layer, however, seem merely to be deviated around the pit canal from their normal course. This deflection is given by Bailey and Vestal as a reason for the radial walls in springwood having a greater fibrillar angle than the tangential walls. Since the central layer normally makes up the greater part of the tracheid wall, its properties are ordinarily designated as those of the entire cell wall.

Preston ('34), in a quantitative study of the organization of

[1] This is the chemical pattern which will be discussed below.

the conifer tracheid cell wall, noted that the fibrillar inclination is greater on radial walls than on tangential walls and that the angle on the radial wall varies between growth rings as a function of average length of springwood tracheid in the ring and of average radial breadth. Maby ('36), using wall checks and pit slits (elongated inner orifices of bordered pits common in summerwood) as indications of structural orientation in tracheids, found for *Tsuga heterophylla* summerwood good positive correlation between angle of inclination with the fiber axis and radial lumen width. Wall thickness did not have good correlation with the angle. This worker also observed that in hemlock springwood fibrillar orientation of the radial wall at the pits is not a good criterion of the orientation in the clear, the average angle for pit slits being about twice that of the checks in the clear. Further, he observed that the orientation at ray crossings was little more than half the angle in the clear. It appears that orientation in springwood tracheids is quite variable and that a true average would embrace several widely different morphological conditions.

That orientation of the fibrillar structure is important in determining strength of fibers is not difficult to conceive; especially is this true in consideration of tensile stresses. It is known, for instance, that the very strong bast fibers of ramie and flax have good fibrillar orientation; that is, the fibrils are almost parallel to the fiber axis.

That the cellulose fibrils of wood (matrix of elongated complexes) are more resistant mechanically than the non-cellulose constituents (interwoven system of isotropic material) may be supported by a brief discussion of the sub-microscopic structure of wood substance. X-ray, polarized light, and swelling technique have demonstrated that the cellulose is oriented parallel to the fibril axis. X-ray diffraction analysis has further shown that the cellulose molecule consists of long chains of anhydroglucose units. The length of the chains and their combinations into structures up to the limits of microscopic visibility have not yet been agreed upon. Meyer ('28) thinks that the chains are about 60 glucose units long, very

strong by reason of primary valence bonds between the glucose units, and that they are held together in bundles (micellae) by secondary valences the high force of which he attributes to the size of the large chain-like molecule. Further, the unsatisfied secondary valences of the outer chains of the micellae constitute a force by which the micelle may adhere to other micellae or may adsorb other molecules. Astbury ('33) and others view the micelle not as a unit structure but merely as a concentration of molecular chains of varying lengths some of which may extend to other micellae forming a continuous cellulose system of indefinite pattern. This concept seems well supported by several different types of physical measurement (Stamm, '36) which give molecular chain lengths far exceeding the unit micellae that have been hypothesized. Below the size of the fibril the problem of the strength of wood is in a theoretical field, but the rapidly developing study of colloidal chemistry may be expected soon to yield methods of obtaining significant submicroscopic data. It must be borne in mind that even if all the factors in microscopic range were controlled there might exist within the fibril structural variables of importance to strength. The non-cellulosic constituents of wood are amorphous, i.e., have no organized molecular forces, and as such must be regarded as secondary in determining strength properties.

High fibrillar angle occurs with low strength in both compression and tension in "compression wood." Pillow and Luxford ('37) have plotted three different strength-density ratios over the sine of the average angle of slope of fibrils for eight specimens of "compression wood" and six specimens of normal wood of air-dry loblolly pine. The average angles were weighted on the basis of springwood-summerwood proportions. The normal wood specimens fell between 14° and 16°, while those of "compression wood" had a range of about 26° to 34°. In spite of the small amount of data and the wide gap in slope of fibrils between normal wood and "compression wood," there appear to be good graphical relationships. Maximum crushing strength and modulus of elasticity in bending

vary almost linearly through "compression wood" to normal wood. Modulus of rupture[1] seems to vary linearly in the "compression wood" region, but the specimens with average angle of 26° appear to be almost as strong as normal wood. This would indicate that ultimate bending strength is not affected until the average fibrillar angle reaches about 25° where it drops off rapidly with increasing angle. Of the three strength properties shown here, modulus of elasticity in bending, on a density basis, is the most sensitive to changes in fibrillar angle and appears to have the least dispersion from the regression line. The bending-strength relationship is the most inexplicable and is also the most unsatisfactory statistically.

The value of using angle of fibrillar orientation for predicting strength may be roughly conceived by comparing the dispersion in the graphical correlation described above, where strength is made dependent upon both specific gravity and fibril angle, with one in which only specific gravity is used as a criterion. The above relationship for compression strength has a dispersion range of about 2000 lbs. / in.^{2} per (gr./cc.)$^{1.25}$, which is equivalent to about 1000 lbs. / in.^{2} for the average specific gravities given in the tables for air-dry loblolly pine specimens. This may be compared with a dispersion range of about 3500 lbs. / in.^{2} as shown in Berkley's ('34) plot of compressive strength over specific gravity for air-dry loblolly pine. Even from this crude comparison and the few data upon which it is based, the fibrillar orientation angle in the central layer of secondary walls of the conifer tracheid gives promise as a quantitative criterion of strength properties of the wood in axial stresses.

It is interesting to note that fibril angle is important in axial compressive strength, in the light of microscopic evidence that cell wall fracture in compression seems to be independent of fibrillar structure. Many workers, notably Robinson ('20) and Bienfait ('26), have reported the so-called "slip lines" occurring in the walls (seen in longitudinal section) of wood fibers that have been subjected to longitudinal compressive

[1] This is a measure of bending strength.

stresses. These lines represent radially sloping tangential planes of shear much as might be expected in tubes of isotropic material which have been subjected to end compression. The angle in a radial plane which these lines make with the cell axis is about 70° according to Bienfait ('26) and Iwanoff ('33). These shear planes extend transversely or at a slight incline around the cell in the wall. They occur concentrated in the region of gross compression failure, and are more widely distributed in green wood that has been stressed than in dry. Robinson ('20) found them in specimens stressed just to the elastic limit and called them indications of initial failure. Koehler ('33) suggests that they are sometimes induced by stresses in the tree and gives their occurrence as one of the causes for brash tension failure.

Robinson ('20) observed that longitudinal tension failure of the fiber wall occurs in planes parallel to the pit slits in the summerwood of normal spruce, but for "brittle" spruce and for a number of harder woods, including pitch pine, the wall fracture is transverse, resembling the compression fracture. Koehler ('33) has shown tension fractures in cells at least partially following the fibrillar orientation, indicating planes of weakness between the fibrils. He concludes that there is a relation between fibril angle and tensile strength, thus:

> Obviously the fibrils must also break somewhere, as well as separate from each other, in order for a fracture to be complete, but the greater the slope of the fibrils the smaller will be the failure within them and the greater the failure between them. If the fibrils should make an angle of nearly 90° with the cell axis, a condition approached in some hardwood vessels, then failure in tension along the grain would be almost entirely between fibrils and the resistance offered by the cell wall would be relatively small.

With regard to regenerated cellulose products, Houwink ('37) suggests that strength may be proportional to micelle length for well-oriented material and supports this by showing that high viscosity of the solution produces strong rayon. Viscosity is thought to be dependent upon micelle length. He illustrates fracture planes for long and short micellae progressing between the micellae and transverse to their orientation. The longer micellae force the fracture line into a more

deviating and longer path than do the short ones, thus providing more area for the distribution of a given stress. This concept may be applied to the anastomosing continuous system of fibrils in natural fibers, by taking as fibril length the longitudinal distance between successive thin places (points of weakness) in the framework. Chemical dissection of fibrils indicates that some points in the framework are less resistant to solvents than others, and there is a possibility that a quantitative structural measurement may be attained through controlled chemical dissection.

The transversely oriented outer layer of fibers has generally been neglected in structural considerations. However, Sonntag ('09) suggested that the difference in the fibril angle between outer and inner (central) wall is important in the mechanism of failure under axial tension. He used as a model two wire helices, one with a flat spiral and one with a steep spiral, the latter inside the former and attached firmly to it at the ends. If this system is stretched longitudinally the inner helix is reduced in diameter more than the outer one and thus pulls away from it. This mechanism was offered as the cause of concentric discontinuities in the cell structure that lead to ultimate fracture of the wood. Thus "compression wood" would be less likely to fail between the outer layer and the central layer than normal wood, because the angle of spiral is more nearly the same in the two layers. However, other structural abnormalities must offset the advantages since "compression wood" is notoriously weak in tension.

The continuous micellar structure of the central layer of the tracheid as elaborated above referred to normal tracheids. Bailey and Kerr ('35) state:

> Conspicuous discontinuities are, however, of not infrequent occurrence in the peculiar tracheids of "compression wood," in so-called gelatinous fibers, in certain types of bast fibers, and in sclerids. This is due to narrow layers of *truly isotropic* material which contain little if any cellulose.

Radio-helical discontinuities or "checks" in the fiber wall are conspicuous and well known in "compression wood." Hartig ('01) illustrated this type of tracheid in some detail. In cross-

section the checks open into the lumen and extend nearly across the central layer. They may branch dichotomously for a short distance near the outer layer. The checks follow the helical orientations of the fibrils, forming radio-helical plates. Hartig also illustrated "tension wood" and showed radial checks which are less profuse and extended from the outer border of the central layer a short way into it. Such checks were not found in fresh wood and were attributed to drying. Another anomalous feature shown for "tension wood" is the occurrence of spiral thickenings on the inner face of the secondary wall (tertiary wall), especially in summerwood (spruce). Hartig also mentioned an extraordinary development of the tertiary wall (inner layer of the secondary wall). He believed this layer to be absent in "compression wood."

CHEMISTRY

A logical method of attack on the strength problems of any structure would entail an examination of the mechanical properties of the various component materials. Unfortunately the materials which compose wood are so intimately associated and apparently so heterogeneous that only general and vague contributions to their individual study can be expected from chemical considerations at present. The constituents of wood are usually grouped in three classes: (1) cellulose, (2) hemicelluloses, (3) lignin. Quantitative determination depends upon solvents used, their concentration, and exact conditions of procedure.

Cellulose is a long-chain polymer whose molecular unit is known but whose chain length is probably variable. Hemicelluloses constitute a mixture of carbohydrates some of which are associated with cellulose in the structural framework and some are not (Norman, '37). Lignin is a non-carbohydrate of unknown chemical structure, and amorphous. Koehler ('33) is of the opinion that the chemical composition of wood is relatively invariable within a species. Ritter and Fleck ('26) found that for a number of species springwood is mostly lower in cellulose and higher in lignin than summerwood. This is explained by the fact that lignin tends to be concentrated in the

"middle lamella" and that the "middle lamella" is a greater proportion of the total wall volume in the thin-walled springwood than in the summerwood. Dadswell and Hawley ('29) reported the difference in chemical composition between brash and tough specimens and between normal wood and "compression wood." Brash Douglas fir of the same density as tough wood had insignificantly greater percentage of cellulose and of lignin than normal. The measure of toughness was 276 cm.-kg. for the tough specimens and 132 cm.-kg. for the brash ones. Although the authors did not observe structural differences in the above specimens they believed that "there may be structural differences that fully account for the strength differences." Comparing normal wood and "compression wood" of Sitka spruce and redwood, they found appreciably lower cellulose content and higher lignin content in "compression wood." Here structural differences were known, but they were "not certain that they were the cause of the variations in strength properties." They also found that the springwood-summerwood relationship of the cellulose and lignin content as shown by Ritter and Fleck was reversed in the case of redwood "compression wood."

These authors (Dadswell and Hawley, '29) are not willing to agree with the concept that has been general among botanists, that lignification is always a source of strength in cellulose plant fiber, nor do they agree with Schorger whom they quote, "It is known that the amount of lignin present in a wood has no direct relation to its mechanical properties." They point out that lignin occurs in a "free condition" in the middle lamella and mixed with relatively large amounts of other material within the fiber, and offer this pertinent observation:

> Variations in the amount of lignin, therefore, have entirely different effects on the strength, depending upon where the variation occurs. Increased lignin content in those parts of the structure where it is mixed with cellulose may increase certain strength properties, while increased lignin content due to increased size of the middle lamella may decrease certain strength properties.

This concept leads us back to the more recent work of Bailey and Kerr ('35, '37). They have disclosed by the use of ap-

propriate solvents on very thin wood sections what might be called the chemical pattern of cellulosic and non-cellulosic constituents of the central layer of the secondary wall. The patterns are explained thus:

> Lamellae of varying porosity or density are due to fluctuations particularly in the number of fibrils per unit area. In other words, the fibrils are loosely aggregated in the more porous lamellae and are closely compacted in the denser lamellae. [Bailey and Kerr, '37]

In a survey of the fibrous cells of higher plants there was shown to be a wide variety of patterns made up of concentric and radial lamellae or zones of various spacing and prominence. In their later paper Bailey and Kerr ('37) have elucidated the distribution patterns in the conifer tracheid which vary from the normal condition to that of "compression wood" as extremes and show intergrading forms. In the broad central layer of the secondary wall of normal tracheids the laminae of varying density are relatively narrow and arranged concentrically, though a weak radial pattern of density may be seen as an undertone. There are no discontinuities in the cellulose system. In the intermediate forms the radial pattern gains prominence, and there may appear to be superimposed concentric and radial distribution. "The wall may exhibit a prevailingly and finely radial pattern." The fibrillar system may still be continuous though "it tends to develop radio-longitudinal cracks in drying. . . ." In the extreme case of "compression wood" the broad inner layer is "composed of coarse, radio-helically oriented plates" which are separated by actual discontinuities in the cellulose system. "Furthermore, the broad inner layer is separated from the narrow first-formed layer of the secondary wall by an isotropic layer of non-cellulosic composition." This last type of wall has no detectable inner wall comparable to that of normal tracheids (Bailey, '38).

Although the chemistry of the cell wall is too obscure for an exact structural analysis, the above information on the distribution of the two main classes of materials, combined with a knowledge of the longitudinal orientation of the wall, should lead to an understanding of the processes of strength resist-

ance in the cell. This follows on the assumption that cellulose is rigid and the non-cellulosic material furnishes planes or regions of weakness. Regarding planes of structural weakness, Bailey ('38) says:

> The more important planes of cleavage in native cellulose are of two types: (a) those that are determined by the visible differences in density and porosity, and (b) those that are governed by submicroscopic factors. The former planes are oriented parallel to the long axis of the porosities and therefore of the fibrils and are effective in dissecting the wall into concentric or radio-helical layers and into elongated aggregates of fibrils. The latter are significant during the chemical dissociation of cellulose into fusiform bodies and other small fragments.

He suggests as a possible indication of submicroscopic planes of weakness the angular ends of hyphal chambers of some fungi working within the cell wall. The cavities are oriented parallel to the fibrils, and the enzyme action takes place on planes corresponding to this orientation and on planes at an angle of 20–25° to this axis without respect to the more minute fibrillar organization. This angle corresponds to that of the planes of action of strong hydrolyzing reagents which dissect fusiform bodies from the wall, and also to that of planes of acetylation of cellulose fibers illustrated by other workers. Whether these planes of chemical action are significant in mechanical dissection is not known. There is a possibility that the saw-tooth tension fracture of the fiber wall that is sometimes observed (Robinson, '20) may be associated with this. In this type of fracture one side of each tooth represents a separation between the fibrils; the other makes an acute angle to it.

MOISTURE CONTENT

The increase of all strength properties due to drying wood substance from the green or saturated condition is pronounced. The theoretical moisture content of the wood at which the fiber walls are saturated and where no free water occurs in the cell spaces is known as the "fiber-saturation point." This concept was put forward by Tiemann ('06). The practical determination of the point was made by plotting the logarithm of a strength property over the moisture content of the wood and

marking the intersection of the straight line representing changing strength values with the horizontal line representing green strength.

The intersection point varies insignificantly for different strength properties and for different specific gravities of the wood, but is considerably different among different species. Wilson ('32) found a variation from 20 to 28 per cent moisture content within a small number of species. In listing these species by progressive fiber-saturation points those of similar structure were found to be grouped.

> The suggestion from this listing is that wood structure of different types, even within a single species, may have different fiber-saturation points or intersection points. [Wilson, '32].

Intersection points may also be obtained from the relation of moisture content to other variables. Wilson found the electrical-conductivity intersection point consistently higher for different species than those obtained by strength measurements, and much less variable. The discrepancies between the two methods are "possibly due to the effect of size and arrangement of elements of the wood structure on the intersection point." It might be added here that the nature of the cell wall must have great influence in determining the intersection point for strength, since the factor actually involved is that moisture content at which the wood substance starts to become more coherent.

Wilson points out that there are two factors involved in the strengthening of wood by drying, (1) the strengthening of the material, and (2) the increase in "compactness of the wood structure" due to change in volume. It is interesting to note in this connection that although the intersection points obtained from strength data agree fairly well with those from shrinkage data, the moisture contents at which shrinkage is first detectable are consistently higher than the first signs of strength increase. This indicates that the mechanism of stiffening lags behind that of shrinking.

The parameter, K, expressing the slope of the line representing the relationship of strength to moisture content below

fiber-saturation point, varies not only among species but for different groups of specimens within a species. It is not associated with specific gravity. Its wide variability among different strength properties is illustrated by Markwardt and Wilson ('35), who have tabulated a number of strength properties with the average change in strength values in terms of per cent for each 1 per cent change in moisture content. Some of these increments for spruce are: modulus of rupture, 4 per cent; modulus of elasticity (static bending), 2 per cent; maximum crushing strength parallel to the grain, 6 per cent; shearing strength parallel to the grain, 3 per cent; tension strength perpendicular to the grain, 1.5 per cent. Kollmann ('36) has published comparable figures for Swedish pine: tensile strength parallel to the grain, 3 per cent, and axial compression (crushing) strength, 4 to 6 per cent.

Pillow and Luxford ('37) found that the strength of "compression wood" does not increase so much in drying as that of normal wood. Among the properties they studied, modulus of elasticity and tension parallel to the grain were exceptional in that their proportional change on drying was not significantly different in the two types of wood. The authors believed that the evidence was inconclusive in the case of tension, due to the insufficient number of tests.

Excessive longitudinal shrinkage is typical of "compression wood," which is known to shrink considerably less than normal wood in transverse directions. The resultant effect, moreover, is a reduced volumetric shrinkage. Hartig ('01) gave an average volumetric shrinkage of 11.545 per cent for "Rothholz" of spruce as against 14.55 per cent for "Weissholz" from the same stem. Trendelenburg ('31) found 8.88 per cent volumetric shrinkage for "Druckholz" of Douglas fir and 10.25 per cent for normal wood. Pillow and Luxford ('37) reported a slightly excessive equilibrium moisture content for "compression wood." In other words, air-dry "compression wood" contains slightly more moisture than normal wood under the same conditions. The difference, from their table of

air-dry properties, amounts to about 0.5 to 1.0 per cent moisture content. The above data indicate that the strength properties of "compression wood" below fiber-saturation point may be abnormal not only because of inherent structural differences but also because of abnormal moisture relations (colloidal properties).

With regard to the mechanism of increase in strength on drying, Stamm ('36) stated:

> The strength of a swollen fiber, in general, increases upon drying. This is explained on the basis of the secondary valence forces between micelles, which in the swollen condition are partially satisfied by mobile water, being brought together on drying and thus satisfying each other. This phenomenon is well illustrated in wood.

He cited the experiments of Lüdtke, in which the tensile strength of regenerated cellulose was found in different liquids:

> In such dry, non-swelling liquids, as benzene, the tensile strength is the same as it is in air. Liquids, such as water, glycerine, and formamide, that cause swelling result in considerable decrease in tensile strength of the fibers. Such liquids as dry ether and alcohol, which have a tendency to remove water from the fibers, cause an increase in the strength of water-swollen fibers.

Russell, Maass and Campbell ('37) show that the strength of paper depends partly upon the area of contact between the fibers. Beating the pulp increases fibrillation, increasing the chances of contact and the strength of the paper. These bonds are held to be purely physical, and are shown to be affected by drying. The tensile strength of paper was increased from 0.69 to 7.28 kg. in drying. The same paper tested in the presence of methyl alcohol sustained 2.32 kg.; in ethyl alcohol, 4.63 kg.; and in propyl alcohol, 5.77 kg. These differences were given as examples of different degrees of loosening of the cellulose-cellulose bond. This suggests a careful reconsideration of the effects of extractives upon the strength of wood.

These workers have offered a theory for the mechanism of drying of cellulose. Although cellulose is not soluble in water, the glucose units of the cellulose chain would be soluble in the regular glucose solvents if they were free. Due to this, cellulose

has "surface solubility" in water. Removal of the water causes crystallization bonds to be made between the surfaces of adjacent cellulose crystallites or single chains. The surfaces are drawn together by surface tension and internal liquid tension, and this constitutes a deformation in the structure.

> Portions of the solid structure brought into contact by such deformations may become bonded together by recrystallization, if the liquid is one that can form such "surface solutions" as were earlier described. Such is the case with cellulose and water. [Russell, et al., '37.]

The above conception of the effect of moisture upon the structural cellulose of natural fibers seems valid, though it may serve as only part of the picture of the mechanism in wood where at least two other broad classes of substance are present. Here there must be secondary valences or "surface solution" bonds between cellulose and other constituents, which may not be affected by water as are the cellulose-cellulose bonds. A possibility suggested by the above theory is the drawing into orientation of some of the short-chain hemicelluloses upon drying, and perhaps their incorporation into the structural system by adsorption.

From this brief discussion of strength-moisture relations it may be concluded that the strength variations among different types of wood of the same anatomical description may not be quantitatively comparable as between green wood and wood dried to any given moisture content. Water must be regarded as a constituent of wood in its natural state, and its removal as comparable to the removal of any constituent. The course of the association of the remaining constituents during the gradual removal of one of them may vary according to the original composition. Thus when a condition is abnormal (statistically infrequent) in green wood it may be more or less so in dry wood at different moisture contents. Until abnormal types of wood can be classified and their drying constants determined, the most valid comparison of properties would seem to be based upon green material. For practical purposes two comparisons must be made, one at a moisture content representing average air-dry conditions.

III. Strength Tests and Physical Measurements

This portion of the study was executed in cooperation with the Department of Civil Engineering, Washington University,[1] and was directed by Professor A. W. Brust of that department.

For the purpose of this study the concept of strength conforms to that in accepted engineering practice. The tests follow standard procedure, with minor modifications as noted, and the results are comparable to other standard engineering studies of small clear specimens of commercial timber. Because of the difficulty of making a thoroughly representative microscopic analysis of specimens of the size used in engineering practice, special attention was given in this study to obtaining specimens of uniform growth ring structures. Uniformity could have been better obtained and the sampling made more certain by reducing the size of the strength specimens. However, as the size of the specimens is reduced there is an increase in testing errors due to undefinable stresses at points of loading and to unequal distribution of stresses by the springwood and summerwood portions of the growth rings. For this reason tests that have been designed by some botanists (Sonntag, '03, and Ursprung, '06) may not be representative of the strength conditions within trees or in large structural members, though the 1 mm.-square sections which they tested are admirably adapted to microscopic examination.

MATERIAL

The type of wood chosen to represent the conifer tracheid was dictated by its availability for personal selection of the green material and by the existence of comparable test data. Further, there were required logs of a diameter that would afford specimens without excessive ring curvature and with

[1] Mr. J. W. Graves, Jr., American Creosoting Company Fellow in Civil Engineering, collaborated in the tests, measurements, and calculations. He has used these physical data as part of the basis for a dissertation entitled "Strength and related properties of various growth structures in shortleaf pine," presented as a requirement for the degree master of science in engineering, June, 1937.

uniformity of growth. These requirements were met fairly well by commercial shortleaf pine produced in central Arkansas.

A. Species.—Commercial shortleaf pine is wood of two species of *Pinus* which are marketed without segregation, namely, shortleaf pine, *Pinus echinata* Mill., and loblolly pine, *Pinus Taeda* L. Since selection of the growth-ring structure of the material entailed a rather wide survey it was not feasible to identify the wood in the tree except for two of the nine logs used. The identification was made on geographic distribution and bark characters. Only two species of pine are native in Arkansas (Turner, '35). They were separated by the color and character of the bark and the presence of "small resin pits 1/16 inch in diameter" (Turner, '37) on the bark of *P. echinata* but not on *P. Taeda.*

B. Source and Selection.—The logs were selected in the storage yard of a sawmill at Sheridan, Arkansas. The source of the wood was within a twenty-five mile radius of this town, which is near the center of the north and south range of shortleaf pine and near the northern limits of the occurrence of loblolly pine, in this part of the southern pine belt.

Departure was taken from the rule of the American Society for Testing Materials ('33), which calls for taking consecutive specimens along cardinal radii of the log section without regard to structure. Selection was made for uniformity of growth, a representative range of ring structure, and for logs of large diameter. After a survey of the available logs the writer marked off a diameter on the selected ones. These were taken into the mill and a 2.5-inch plank was cut through each log at the marked diameter. Table I gives a brief description of the logs, and pl. 2 shows the structure of the planks. After the planks were dipped in "Dowicide" (an aqueous fungicide), they were bound face-to-face in two packages and shipped immediately to St. Louis.

C. Care and Preparation of the Specimens.—Two days after sawing, the planks were placed in a moist cold-storage room

TABLE I
DESCRIPTION OF LOGS

Log No.	Species	Number of growth rings	Diameter (inches)
1	Loblolly *(Pinus Taeda)*	85	20
2	Loblolly *(Pinus Taeda)*	60	22 Butt log
3	Loblolly *(Pinus Taeda)*	30	16
4	Shortleaf *(Pinus echinata)*	75	16 Butt log
5	Shortleaf *(Pinus echinata)*	200	28 Virgin growth
6	Shortleaf *(Pinus echinata)*	160	34 Virgin growth
7	Shortleaf *(Pinus echinata)*	100	19 Butt log
8	Shortleaf *(Pinus echinata)*	55	14
9	Shortleaf *(Pinus echinata)*	80	16 Butt log

where the temperature varied between 32 and 38° F. The planks were immediately cut into two equal lengths, and one half of each was removed to the laboratory, cut into sticks approximately 2.25 inches wide, and stacked for drying. The air-dry sticks were not cut into specimens until they had reached constant weight. The green halves of the planks were removed from cold storage, a plank at a time, and each was prepared and tested within three days.

In marking the planks for cutting into 2.25-inch sticks an attempt was made to include only uniform growth within each cross-section, and the cuts were made, as far as practical, parallel to the growth rings longitudinally The longitudinal rows of specimens included approximately the same growth rings in both the green and dry sections of the planks. The rough-sawn sticks were dressed by hand to uniform cross-sections approximately 2″ by 2 ″, with an open rotary planer (jointer). In this operation an attempt was made to true the sticks with the grain on all faces. The compression specimens were merely 6-inch sections cut from the dressed sticks. The tension specimens (fig. 3) were cut to shape on a band-saw, and then the small center test sections were dressed with a straight blade cutter head attached to a drill press as a shaper (pl. 1, fig. 1).

D. Designations of Specimens.—Each specimen is identified by a trinomial designation; for example, 4-A-7. The first num-

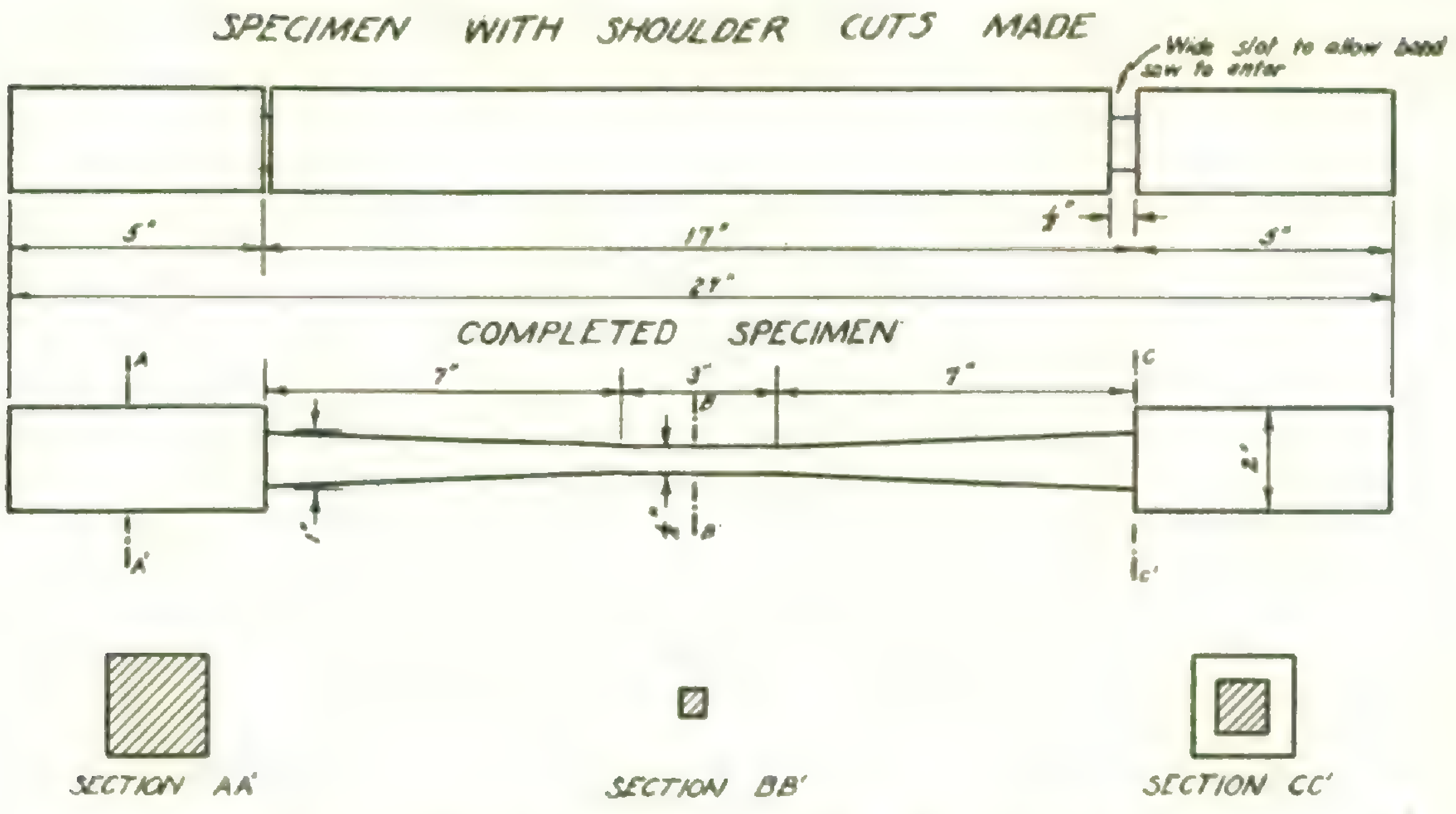

Fig. 3. Design of tension specimen used in this study.

ber refers to the log and the last number refers to the stick or the longitudinal row of specimens (pl. 2). The letter between the numbers designates the section of the original plank, cut in alphabetical order from the large end of the log. Each section was about 40 inches long, and the specimens were cut from it according to the suitability of the grain. Only specimens with identical designations may be regarded as matched, although those in the same longitudinal row may have been influenced by the same general growth conditions. The influence of "butt swell" upon the wood may be present in the "A" and "B" sections of Logs 2, 4, 7 and 9, so that these sections may not be comparable to other sections in the same row. There were bending tests and longitudinal shear tests made from this raw material in addition to the tension and compression tests reported here.

TESTS AND MEASUREMENTS

Wood is most often stressed in bending, in compression parallel to the grain, or in compression perpendicular to the grain, and there are adequate test data available in these strength categories. Though wood is strongest in tension parallel to the grain, its use in this manner is limited by its strength in shear along the grain, and since this is of very low order com-

paratively little attention has been given by engineers to the longitudinal tension test. The recent introduction of "timber connectors," devices for increasing the area of shear at the ends of tension members, should stimulate more work on tensile strength in the future, especially in connection with elastic properties and in consideration of abnormal types of wood.

For the present study the bending test has not been used because the applied force is resolved into longitudinal compression stresses, tension stresses, and shear stresses, which are unevenly distributed and undefinable for any certain area chosen for microscopic examination. The test for shear parallel with the grain would probably make a fruitful subject for the study of variability in wood, if it were not for the fact that no test has been devised in which longitudinal shear is known to be exclusively active.

The tension test and the compression test parallel to the grain are most easily understood, and the type of internal stress working on the individual fiber may be inferred. The fibers here are put to their best advantage, affording the best possible comparison. The stress in these tests is based on the transverse section of the wood which most truly represents the volumetric characteristics, i.e., descriptions and control data taken from the end section apply to the region of actual failure.

A. Tension Tests.—For the same reason that wood is rarely used as tension members in structural work, the testing of small clear specimens in tension is difficult. Since wood is about twenty times as strong in longitudinal tension as it is in longitudinal shear, the specimens must be designed to create enough longitudinal shear area to bear the load that will break the small section in the middle of the length (fig. 3, BB′). Further, there must be provided a gradual reduction in section area from the shoulder (CC′) to the test section to reduce the possibility of a concentration of internal stresses that will cause failure outside of the test section. Kollmann ('36) has illustrated a wide variety of tension-specimen designs proposed by different workers and used in different countries. The type of

specimen used in this study is identical with the standard in American practice except that the test section is reduced from six inches to three inches in length, and from $(5/8)^2$ inch to $(1/2)^2$ inch in sectional area. This specimen has been found to have the advantage of being less subject to damaging stresses in handling and less likely to fail in shear due to slight spiral or cross grain. In spite of the care taken in preparation, some of the specimens failed entirely in one of the tapered shanks, or failed in tension partially in the test section and partially in the shank with longitudinal shear connecting these fractures. When fracture did not occur entirely within the test section it may be assumed that the maximum stress given is conservative, i.e., the section had not yet sustained its breaking load when failure occurred elsewhere and ended the test. The elastic data, however, can always be taken as valid, since the strain measurements were confined to a two-inch portion of the measured section and were not affected by stresses and strains in other parts of the specimens.

The area of the test section was computed from micrometer measurements to 0.001 inch. Testing was conducted on an Amsler hydraulic testing machine (pl. 1, fig. 2). The load was applied to the shoulders of the specimens (fig. 3, CC′) through split steel rings with one-inch-square center openings which fitted about the shanks. These in turn rested upon spherically seated rings which transferred the load to the head blocks of the machine. Load was applied at an average speed of 0.007 inch per minute. Strain was measured with a "Last Word" extensometer reading to 0.0001 inch. This device measured extension over the middle two inches of the three-inch test section.

B. Compression Test.—The specimens for this test deviated from American standard practice in being six inches in length instead of eight inches, although they conformed to the 2″ × 2″ cross-section required. The ends of the specimens were sanded smooth and square, and length was measured to 0.01 inch with a steel scale; section dimensions were measured by micrometer to 0.001 inch. These tests were made on a Riehle three-screw

testing machine of 150,000 pounds capacity, equipped with a spherically seated head block. The testing speed was 0.024 inch per minute. Strain was taken as the distance moved by the head block and was measured with an Ames dial reading to 0.0005 inch. This method deviates from the recommendations of the American Society for Testing Materials which require strain to be measured between points six inches apart in the middle of an eight-inch specimen. The unit deformation over the full length has been reported to be consistently larger than that derived from the recommended method, and, further, the modulus of elasticity based on full-length deformation is better related to maximum strength (Brust and Berkley, '35).

C. Specific Gravity Determinations.—Specimens for specific gravity applying to the compression specimens were cut from the sticks near them. In the case of the tension tests, specific-gravity specimens were cut from unbroken portions of the 0.5-inch-square test sections of the tension specimens. If the test section had been shattered, a block was cut from identical growth rings traced into the shank.

The data for the determinations were obtained by weighing the blocks in air and in water, with a correction made for the water absorbed during the immersed weighing. Immersed weighing was done with a balance on which a weighted calibrated wire frame was substituted for one of the hanging pans. Specific-gravity values were referred to volumes as tested except for the air-dry tension test. It was found impossible to weigh accurately the dry two-gram blocks in water because of the air bubbles collecting on the wood due to displaced air. Specific-gravity determinations of both green and dry tension specimens were based upon their volumes in a resoaked condition. All specific gravities were corrected for benzol-soluble extractives; this tends to equate heartwood and sapwood.

D. Per Cent Summerwood.—Although the percentage of summerwood is not used as a correlation factor, a visual estimation is recorded for the compression test specimens, and a

value for each of the tension pieces was obtained by planimetering. This latter value represents the percentage of summerwood in the entire cross-section and may differ considerably from the proportion in the average growth ring, especially in wide-ringed material.

E. Moisture Content.—For green specimens the moisture content was derived from the specific-gravity specimen in the stick section of the same designation. This constituted merely a check against the possibility of the tested wood having dried below the fiber-saturation point which Berkley ('34) found to be 22.5 per cent for southern pine. One-inch sections were cut from the air-dry specimens and weighed immediately after each strength test. For the tension specimens this sample was taken from the large end of one of the tapered shanks.

F. Longitudinal Shrinkage.—Since this is the only physical property on the basis of which "compression wood" may be quantitatively segregated from normal wood, a series of these measurements was made in this study. For this purpose a four-inch section was taken at the mid-point of the original plank for each longitudinal row of specimens. This sample may be assumed to be fairly representative of the "B" and "C" specimens, but it is likely to indicate less shrinkage than is actually present in the "A" specimens and more than the "D" and "E" specimens. Especially is this so for the butt logs 2, 4, 7, and 9. This follows the findings of Pillow and Luxford ('37) that "compression wood" is much more frequent in the lower seventeen feet of shortleaf pine trees from Arkansas than at greater heights.

A 1″ × 1″ × 4″-piece was cut square with the growth rings from the 2″ × 2″ × 4″-sample, the ends sanded, and the center points marked. The difference in length from green to oven-dry was obtained by means of dial gauge reading to 0.0005 inch.

The physical data are given in columns 2 to 10 in tables II to V. The specimens represented here are those remaining after careful inspection had eliminated those with irregularities in gross character that might influence the data on ultimate

strength or stiffness. The strength figures given represent two aspects of the resistance to stress: (1) the maximum load that the material is able to bear, and (2) the resistance to deformation or the stiffness of the material. The modulus of elasticity represents the load required to lengthen or shorten a specimen, per unit length of the loading axis *during the time the material remains elastic.* This then is a measure of the stiffness of the material within the range where releasing the load will return it to its original form (length). Stiffness is included in the general term "strength"; however, in the indexes given in this paper "strength" indicates maximum or ultimate strength, and "stiffness" refers to the property evaluated by modulus of elasticity.

The strength-density index and the stiffness-density index of the wood refer strength and stiffness to factors other than specific gravity. If these indexes were multiplied by the specific gravity of wood substance they would give the stresses for the wood substance according to the argument presented above under "Density."

IV. Analysis

THE EFFECT OF GROWTH RING WIDTH

It may not be assumed from fig. 2 that growth rate in itself has an influence on the strength-density index, since no data are given on the variability within any growth-rate range. It is indicated that low strength is more likely to occur at more rapid growth rates regardless of specific gravity. The low average strength in wide-ring classes might be due merely to the more frequent occurrence of abnormal wood in them with random choice of specimen.

Figs. 4 to 9 present the distribution of strength- and stiffness-density indexes according to growth rate for the material tested. Considering the distribution of the individual specimens it is obvious that the correlation between axial strength properties and growth rate is poor. Large variations occur well within the growth-rate range acceptable for structural purposes, and many wide-ringed specimens show excellent

TABLE II

AXIAL TENSION TESTS, GREEN

(1) Specimen	(2) Specific gravity based on green volume*	(3) Moisture content in per cent of oven-dry weight	(4) Growth rings per inch	(5) Summerwood in per cent of cross-section area of specimen	(6) Longitudinal shrinkage in per cent of green length†	(7) Ultimate tensile strength	(8) Strength-density index, col. (7) / col. (2)	(9) Modulus of elasticity	(10) Stiffness-density index, col. (9) / col. (2)	(11) Average angle of fibrillar orientation in summerwood	
	(gr./cc.)	(%)		(%)	(%)	(lbs./in.²)	(lbs./in.²) / (gr./cc.)	(1000 lbs./in.²)	(1000 lbs./in.²) / (gr./cc.)	(degrees)	(sine)
1-B-1	.456	118	6.1	38	.051	*12,180***	26,750	1,530	3,360	8.2	.143
2-C-2	.531	109	4.0	50	.025	*13,000*	24,500	2,260	4,260	7.0	.122
2-C-3	.539	110	6.4	55	.082	*16,000*	29,700	1,870	3,470	6.5	.113
2-C-7	.491	114	5.4	54	.416	11,300	23,000	1,520	3,100	14.0	.242
3-A-1	.480	134	3.7	33	.251	8,750	18,220	1,175	2,450	15.2	.262
3-B-6	.396	117	6.3	22	.100	10,700	27,000	1,270	3,210	11.1	.193
4-D-2	.418	36	10.2	27	.088	*14,150*	33,900	1,830	4,380	8.6	.150
4-C-3	.440	25	6.9	34	.244	6,830	15,500	935	2,120	19.6	.335
4-C-4	.528	105	4.9	62	.266	10,100	19,100	1,060	2,050	19.6	.335
4-C-5	.456	126	9.2	46	.013	8,650	19,000	911	2,000	20.8	.355
6-B-2	.501	101	7.6	47	.051	14,250	28,450	2,940	5,870	8.0	.139
7-A-2	.549	85	12.0	38	‡– .050	17,000	31,000	1,990	3,625	13.6	.235
7-A-4	.600	78	6.5	52	.138	10,140	16,900	1,160	1,934	23.0	.391
7-A-6	.566	78	15.4	51	.013	*18,650*	33,000	2,890	5,110	11.5	.199
8-C-1	.448	129	6.8	35	.089	14,400	32,200	1,440	3,220	14.7	.254
8-C-2	.531	118	7.0	44	.063	*18,650*	35,150	1,955	3,680	10.5	.182
8-C-4	.568	114	6.7	51	.025	*18,500*	32,600	2,650	4,670	9.2	.160
9-A-1	.493	117	3.3	48	– .038	11,250	22,800	1,470	2,980	14.3	.247
9-C-1	.501	120	4.6	46	.089	17,300	34,600	2,035	4,060	7.0	.122
9-A-2	.550	105	3.2	58	– .037	*10,180*	18,500	1,155	2,100	19.0	.326
9-C-2	.503	122	5.9	39	.088	*15,860*	31,600	2,200	4,370	8.0	.139
9-A-3	.491	91	8.8	69	.728	7,140	14,540	719	1,462	32.2	.533
9-C-3	.485	116	5.6	45	.278	*15,900*	32,800	1,990	4,110	14.9	.257
9-A-4	.540	106	4.0	81	1.340	7,500	13,900	667	1,236	30.5	.508
9-C-4	.427	123	4.3	35	.478	8,990	21,000	1,070	2,505	24.1	.408

* Specific gravity is corrected for benzol extractive.
† The specimens were taken between the "B" and "C" strength specimens.
‡ (–) signifies an extension in drying.
** Italics indicate fracture occurred outside the measured section of the specimen; this value may be low.

TABLE III

AXIAL TENSION TESTS, AIR-DRY

(1) Specimen	(2) Specific gravity based on green volume*	(3) Moisture content in per cent of oven-dry weight	(4) Growth rings per inch	(5) Summerwood in per cent of cross-section area of specimen	(6) Longitudinal shrinkage in per cent of green length†	(7) Ultimate tensile strength	(8) Strength-density index, col. (7) / col. (2)	(9) Modulus of elasticity	(10) Stiffness-density index, col. (9) / col. (2)	(11) Average angle of fibrillar orientation in summerwood	
	(gr./cc.)	(%)		(%)	(%)	(lbs./in.²)	(lbs./in.²) / (gr./cc.)	(1000 lbs./in.²)	(1000 lbs./in.²) / (gr./cc.)	(degrees)	(sine)
1-D-1	.407	10.0	10.1	–	.051	*15,950***	39,200	2,300	5,650	7.7	.134
1-C-3	.511	10.4	7.2	55	1.500	13,000	25,400	1,428	2,650	19.6	.335
1-C-4	.501	10.4	4.6	67	.754	12,900	25,750	1,230	2,455	22.9	.389
1-C-5	.523	10.1	4.6	61	.839	10,560	20,200	1,206	2,306	26.4	.445
2-B-2	.534	10.1	3.2	35	.025	13,930	26,000	2,170	4,060	13.4	.232
2-A-3	.524	10.9	4.4	70	.062	18,400	35,100	1,640	3,130	20.3	.347
2-A-6	.506	10.6	3.3	84	.151	10,800	21,350	1,590	3,120	33.2	.548
2-B-7	.480	10.4	5.4	31	.200	12,250	25,500	1,610	3,355	17.6	.302
3-C-1	.426	9.6	3.4	37	.251	19,850	46,600	2,500	5,870	13.8	.238
3-C-2	.519	9.8	3.0	69	.062	17,400	33,500	1,875	3,610	19.9	.340
3-D-6	.432	9.8	4.8	71	.020	13,700	31,700	1,640	3,800	18.0	.309
4-A-1	.502	10.9	12.0	36	.076	*22,500*	44,800	2,920	5,810	8.0	.139
4-A-3	.497	10.3	5.6	30	.244	*14,500*	29,200	1,895	3,810	14.8	.255
4-A-5	.451	9.9	7.4	29	.013	14,800	32,800	1,510	3,350	17.7	.304
5-D-3	.495	10.3	18.4	31	.063	14,600	29,500	2,790	5,640	4.8	.084
5-D-4	.497	10.4	18.0	34	.005	13,700	27,600	2,140	4,300	6.2	.108
6-A-2	.491	9.0	7.3	45	.051	*16,100*	32,800	2,660	5,420	12.8	.222
7-B-2	.538	10.8	10.1	48	‡– .051	*13,100*	24,350	1,770	3,290	17.9	.308
7-B-4	.416	10.2	9.4	27	.138	13,700	32,900	1,540	3,700	17.2	.296
7-B-6	.546	10.4	12.1	47	.013	18,400	33,700	2,440	4,460	11.4	.198
8-A-1	.506	9.2	7.2	46	.069	16,970	33,500	1,730	3,420	20.5	.350
8-A-2	.560	9.6	7.8	56	.063	*16,800*	30,000	2,130	3,800	17.6	.302
8-B-3	.592	9.7	7.3	60	.057	22,100	37,300	2,440	4,120	17.4	.299
8-A-4	.482	8.7	6.7	36	.025	*13,200*	27,400	1,665	3,460	19.0	.326
9-E-1	.455	8.8	4.0	–	.089	*14,400*	31,650	2,460	5,410	8.6	.150
9-D-4	.451	8.9	4.2	49	.476	11,300	25,050	1,327	2,940	23.2	.394

* Specific gravity was corrected by deducting benzol extractive.
† The specimens were taken between the "B" and "C" strength specimens.
‡ (–) signifies an extension in drying.
** Italics indicate fracture occurred outside the measured section of the specimen; this value may be low.

TABLE IV

AXIAL COMPRESSION TESTS, GREEN

(1) Specimen	(2) Specific gravity based on green volume*	(3) Moisture content in per cent of oven-dry weight	(4) Growth rings per inch	(5) Estimated width of summerwood in per cent of growth ring width	(6) Longitudinal shrinkage in per cent of green length†	(7) Maximum crushing strength	(8) Strength-density index, col. (7) / col. (2)	(9) Modulus of elasticity	(10) Stiffness-density index, col. (9) / col. (2)	(11) Average angle of fibrillar orientation in summerwood	
	(gr./cc.)	(%)		(%)	(%)	(lbs./in.^{2})	(lbs./in.^{2}) / (gr./cc.)	(1000 lbs./in.^{2})	(1000 lbs./in.^{2}) / (gr./cc.)	(degrees)	(sine)
1-B-1	.444	118	7.0	25	.051	3,360	7,570	776	1,748	8.4	.146
1-A-2	.575	35	6.0	75	1.640	4,190	7,290	505	879	–	–
1-B-4	.569	60	3.7	60	.754	3,780	6,640	604	1,060	28.8	.482
1-B-5	.506	68	5.0	55	.839	3,440	6,800	615	1,215	–	–
2-D-1	.458	124	3.9	30	.025	3,420	7,470	729	1,590	10.2	.177
2-D-2	.487	109	4.4	35	.025	3,810	7,820	790	1,620	10.8	.187
2-D-3	.478	110	5.9	30	.062	3,750	7,850	912	1,910	6.0	.105
3-A-1	.434	134	4.1	45	.251	3,380	7,790	775	1,784	12.4	.215
4-C-1	.433	120	12.6	25	.076	3,770	8,710	925	2,135	7.2	.125
4-D-2	.538	36	8.9	25	.088	3,750	6,970	750	1,393	7.0	.122
5-B-1	.544	85	18.6	50	.013	3,910	7,190	789	1,450	8.6	.150
5-B-2	.566	65	17.5	45	.078	4,380	7,740	904	1,598	8.7	.151
5-B-3	.535	29	22.2	40	.083	5,220	9,760	902	1,687	7.0	.122
5-B-4	.521	31	17.5	35	.005	4,450	8,540	1,100	2,109	6.8	.118
6-B-2	.476	101	8.3	50	.051	3,380	7,110	878	1,847	8.0	.139
6-B-6	.453	30	4.7	50	.040	3,140	6,930	610	1,347	21.3	.363
6-B-7	.445	26	5.0	40	.086	3,170	7,120	654	1,469	19.8	.339
7-A-2	.545	85	11.9	50	‡– .050	4,000	7,340	1,020	1,871	10.6	.184
7-A-3	.543	56	11.4	45	– .089	3,330	6,130	546	1,006	20.0	.342

TABLE IV (Continued)

(1) Specimen	(2) Specific gravity based on green volume*	(3) Moisture content in per cent of oven-dry weight	(4) Growth rings per inch	(5) Estimated width of summerwood in per cent of growth ring width	(6) Longitudinal shrinkage in per cent of green length†	(7) Maximum crushing strength	(8) Strength-density index, col. (7) / col. (2)	(9) Modulus of elasticity	(10) Stiffness-density index, col. (9) / col. (2)	(11) Average angle of fibrillar orientation in summerwood	
	(gr./cc.)	(%)		(%)	(%)	(lbs./in.^{2})	(lbs./in.^{2}) / (gr./cc.)	(1000 lbs./in.^{2})	(1000 lbs./in.^{2}) / (gr./cc.)	(degrees)	(sine)
7-A-4	.592	78	6.0	50	.138	3,840	6,480	639	1,080	27.0	.454
7-A-5	.588	80	10.5	60	– .037	4,550	7,740	894	1,520	12.0	.208
7-A-6	.557	78	12.7	45	.013	4,260	7,640	828	1,484	11.2	.194
8-C-1	.469	129	8.6	40	.089	4,230	9,020	945	2,015	11.4	.198
8-C-3	.511	104	7.3	40	.057	4,590	8,990	937	1,633	12.2	.211
8-C-4	.499	114	7.6	40	.025	4,850	9,720	964	1,930	12.1	.210
9-A-1	.471	117	4.6	35	– .038	3,460	7,350	684	1,452	10.2	.177
9-C-1	.462	120	4.4	35	.089	3,600	7,790	772	1,670	8.0	.139
9-A-3	.513	91	3.8	50	.728	3,250	6,340	491	957	26.6	.448
9-A-4	.477	106	4.1	45	1.340	3,320	6,960	501	1,050	29.2	.488

* Specific gravity is corrected for benzol extractive.
† The shrinkage specimens were taken between the "B" and "C" strength specimens.
‡ (–) signifies an extension in drying.

TABLE V

AXIAL COMPRESSION TESTS, AIR-DRY

(1) Specimen	(2) Specific gravity based on air-dry volume*	(3) Moisture content in per cent of oven-dry weight	(4) Growth rings per inch	(5) Estimated width of summerwood in per cent of growth ring width	(6) Longitudinal shrinkage in per cent of green length†	(7) Maximum crushing strength	(8) Strength-density index, col. (7) / col. (2)	(9) Modulus of elasticity	(10) Stiffness-density index, col. (9) / col. (2)	(11) Average angle of fibrillar orientation in summerwood	
	(gr./cc.)	(%)		(%)	(%)	(lbs./in.²)	(lbs./in.²) / (gr./cc.)	(1000 lbs./in.²)	(1000 lbs./in.²) / (gr./cc.)	(degrees)	(sine)
1-D-1	.522	7.3	11.0	30	.051	8,260	15,800	1,440	2,760	6.2	.108
1-D-2	.570	8.3	7.1	20	1.640	7,650	13,420	1,052	1,848	27.9	.468
1-C-4	.558	7.4	4.6	60	.754	7,720	13,840	1,050	1,880	27.6	.463
1-C-5	.568	6.8	5.3	60	.839	7,500	13,200	1,010	1,780	29.8	.497
2-B-1	.580	7.3	5.4	35	.025	9,150	15,780	1,520	2,620	9.5	.165
2-B-2	.618	7.8	4.3	35	.025	9,630	15,580	1,568	2,540	8.0	.139
2-A-3	.616	8.8	5.4	35	.062	9,110	14,800	1,505	2,445	12.8	.222
2-A-6	.561	7.7	4.2	35	.151	7,490	13,330	1,000	1,785	25.2	.426
2-B-7	.586	7.8	5.2	40	.200	8,120	13,850	1,150	1,962	21.1	.360
2-A-8	.560	7.9	4.7	35	.123	8,470	15,120	1,467	2,620	14.1	.244
3-C-1	.502	8.7	4.7	30	.251	7,970	15,870	1,574	3,140	6.9	.120
3-C-2	.482	8.6	3.5	35	.062	8,020	16,620	1,450	3,005	12.0	.208
3-C-4	.451	8.6	4.0	20	.018	7,220	16,000	1,380	3,060	11.8	.205
3-D-5	.512	9.0	3.2	30	.020	6,970	13,600	1,250	2,440	14.3	.247
3-D-6	.488	8.4	4.7	20	.100	7,260	14,900	1,305	2,675	13.6	.235
4-A-1	.526	7.7	10.9	35	.076	9,500	18,050	1,770	3,360	8.7	.151
4-B-2	.489	8.4	8.6	35	.088	9,350	19,100	1,780	3,640	9.0	.156
4-A-4	.566	8.5	5.2	35	.266	9,070	16,000	1,380	2,440	16.0	.276
5-D-1	.565	8.6	24.4	40	.013	8,900	15,750	1,671	2,960	7.2	.125
5-D-2	.667	8.9	20.9	35	.076	10,530	15,800	1,980	2,970	5.4	.094

TABLE V (Continued)

(1) Specimen	(2) Specific gravity based on air-dry volume*	(3) Moisture content in per cent of oven-dry weight	(4) Growth rings per inch	(5) Estimated width of summerwood in per cent of growth ring width	(6) Longitudinal shrinkage in per cent of green length†	(7) Maximum crushing strength	(8) Strength-density index, col. (7) / col. (2)	(9) Modulus of elasticity	(10) Stiffness-density index, col. (9) / col. (2)	(11) Average angle of fibrillar orientation in summerwood	
	(gr./cc.)	(%)		(%)	(%)	(lbs./in.²)	(lbs./in.²) / (gr./cc.)	(1000 lbs./in.²)	(1000 lbs./in.²) / (gr./cc.)	(degrees)	(sine)
5-D-3	.585	9.2	21.2	30	.063	10,100	17,260	1,775	3,040	5.0	.087
5-C-5	.562	9.3	16.2	35	.013	8,330	14,800	1,500	2,665	13.4	.232
6-A-2	.548	8.9	9.4	45	.051	8,500	15,500	1,735	3,170	7.1	.124
6-A-3	.520	9.0	5.9	35	.089	7,990	15,350	1,610	3,100	7.2	.125
6-A-6	.523	8.7	5.5	35	.040	7,000	13,400	1,255	2,400	15.0	.259
6-A-7	.447	11.1	4.4	35	.086	7,040	15,720	1,184	2,650	19.0	.326
7-B-1	.584	9.3	14.8	35	.025	8,840	15,120	1,776	3,040	11.6	.201
7-B-2	.635	9.8	9.2	45	‡– .050	9,050	14,240	1,700	2,680	14.4	.249
7-B-3	.586	10.1	7.4	30	– .089	8,140	13,900	1,370	2,340	13.4	.232
7-B-4	.549	9.9	7.3	30	.138	7,300	13,300	1,160	2,110	17.5	.301
8-A-1	.572	8.1	7.9	45	.084	8,420	14,700	1,270	2,220	17.8	.306
8-A-2	.637	7.3	8.1	50	.063	8,620	13,520	1,420	2,230	19.3	.331
8-A-4	.616	7.8	7.3	45	.025	8,590	13,930	1,380	2,240	18.9	.324
9-E-1	.497	9.1	5.8	30	.089	7,740	15,560	1,700	3,420	4.6	.080
9-E-3	.509	9.2	8.6	40	.278	6,740	13,230	1,160	2,280	20.6	.352
9-D-4	.484	9.3	4.6	40	.478	6,400	13,200	985	2,033	24.0	.407

* Specific gravity is corrected for benzol extractive.
† The shrinkage specimens were taken between the "B" and "C" strength specimens.
‡ (–) signifies an extension in drying.

strength properties for their densities. Although a larger random representation would perhaps show that there is a concentration of "abnormal" material in the range of wide rings, it is not indicated that width of growth ring in itself is a considerable factor in the resistance of solid material of the wood to axial stresses.

Since data on tension strength are rather rare in the literature these charts are of interest in comparing the tension and compression stresses under different moisture conditions considering the data as groups of specimens from the same lot of wood. Any solution for the true mechanism of stress resistance must consider the facts shown here: that in the green condition axial tension strength of the wood substance is more than twice as great as axial compression strength; and that drying has less effect upon tension strength and stiffness than upon compression strength and stiffness.

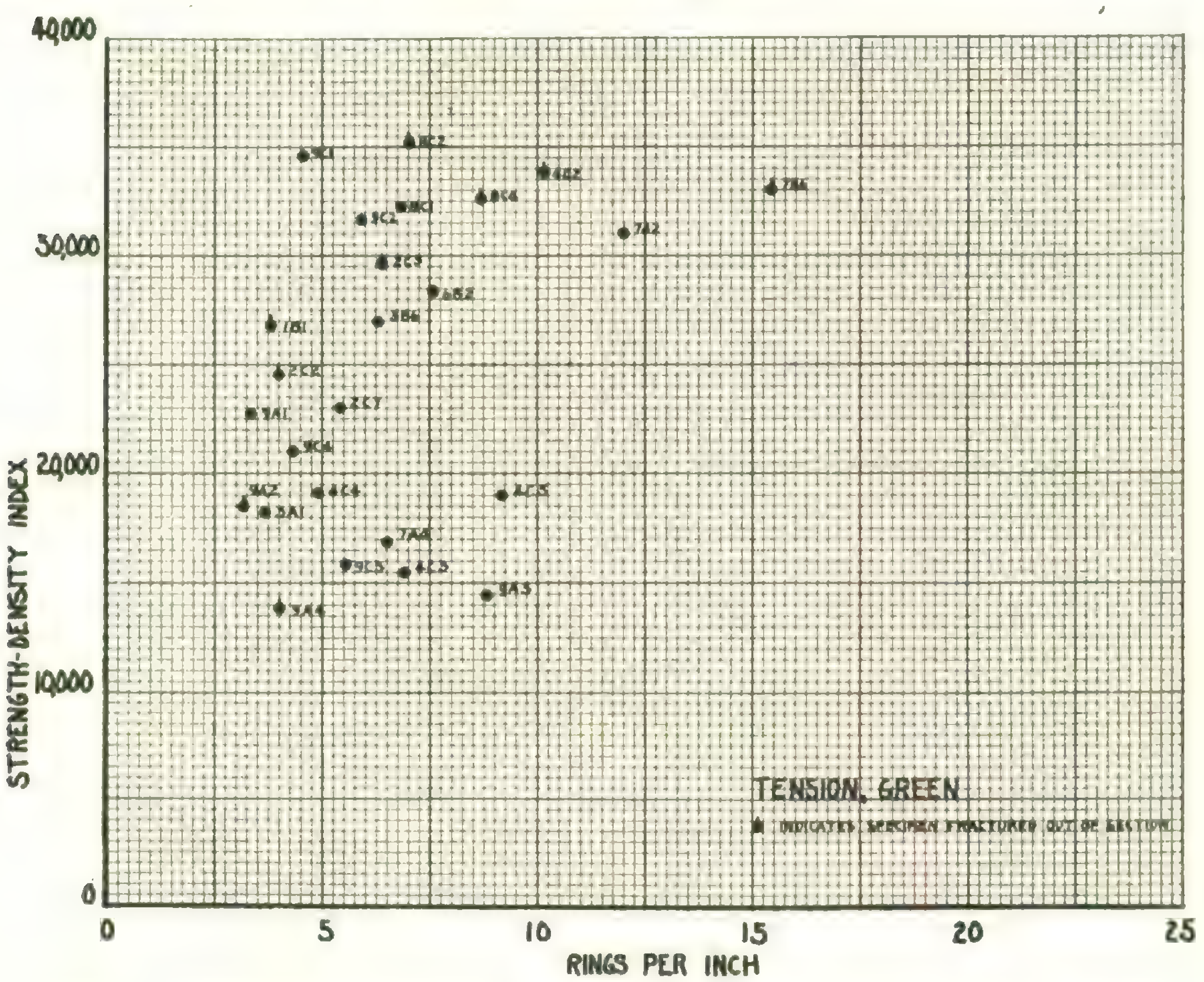

Fig. 4. Axial strength-density index (ultimate strength ÷ specific gravity) plotted over growth rate for green specimens.

The normality of the wood used in this study may be judged by comparison with the average data given by Markwardt and Wilson ('35) for *Pinus echinata,* taken near Malvern, Arkansas. The average maximum crushing strength in compression parallel to the grain in green condition was 3570 lbs. per sq. in.; the average specific gravity, at test, was 0.477, and the average number of rings per inch was 13.4. These data

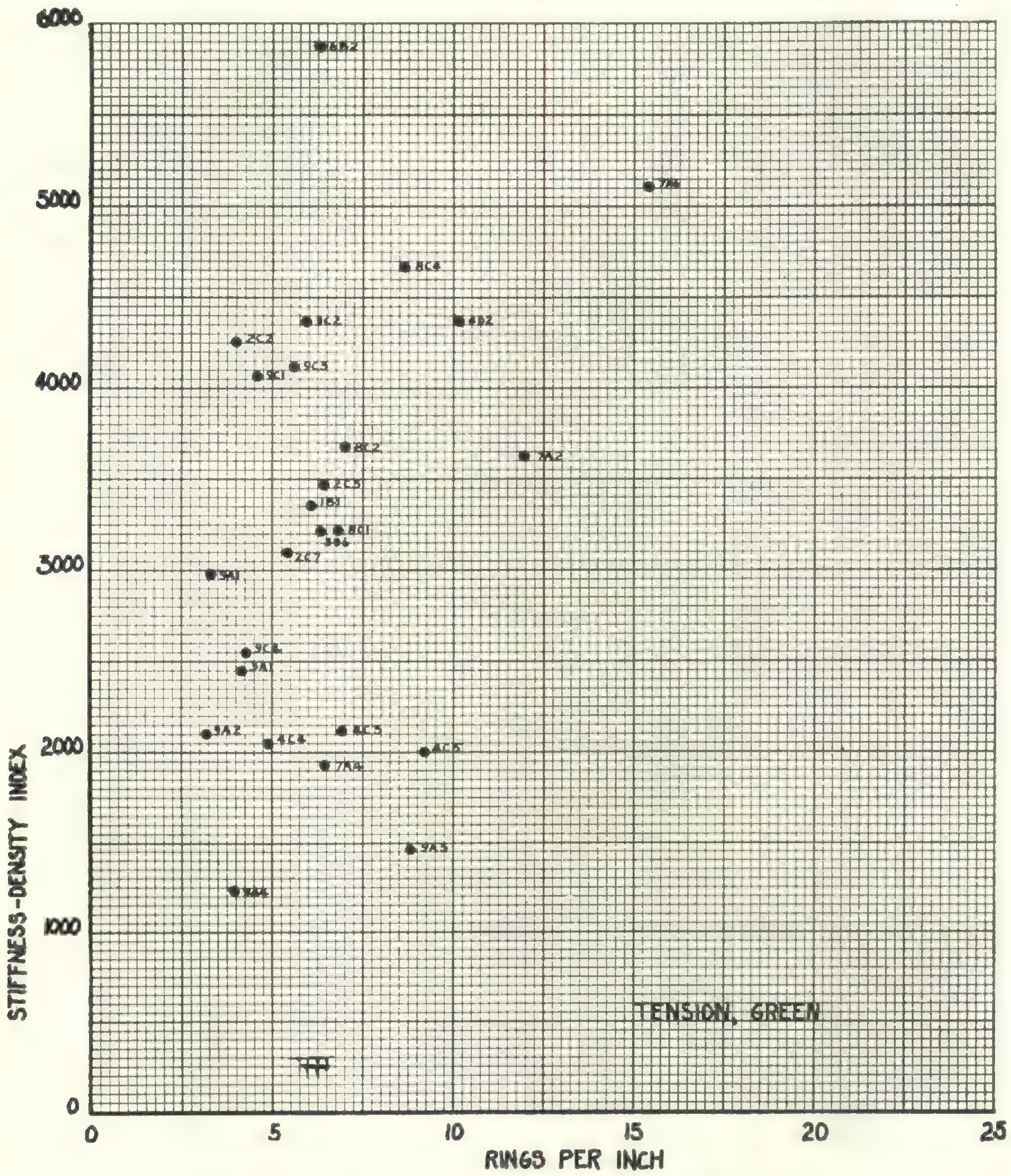

Fig. 5. Axial tension stiffness-density index (modulus of elasticity ÷ specific gravity) plotted over growth rate for green specimens.

are comparable to those of the compression tests used in this study and when calculated into an average strength-density index and plotted in fig. 6 are seen to fit quite well. The point is represented by the X mark at 13.4 rings per inch.

CORRELATION OF STRENGTH AND STIFFNESS WITH FIBRILLAR ORIENTATION

Since low strength for its density is known to be accompanied by high angle of fibrillar orientation in "compression

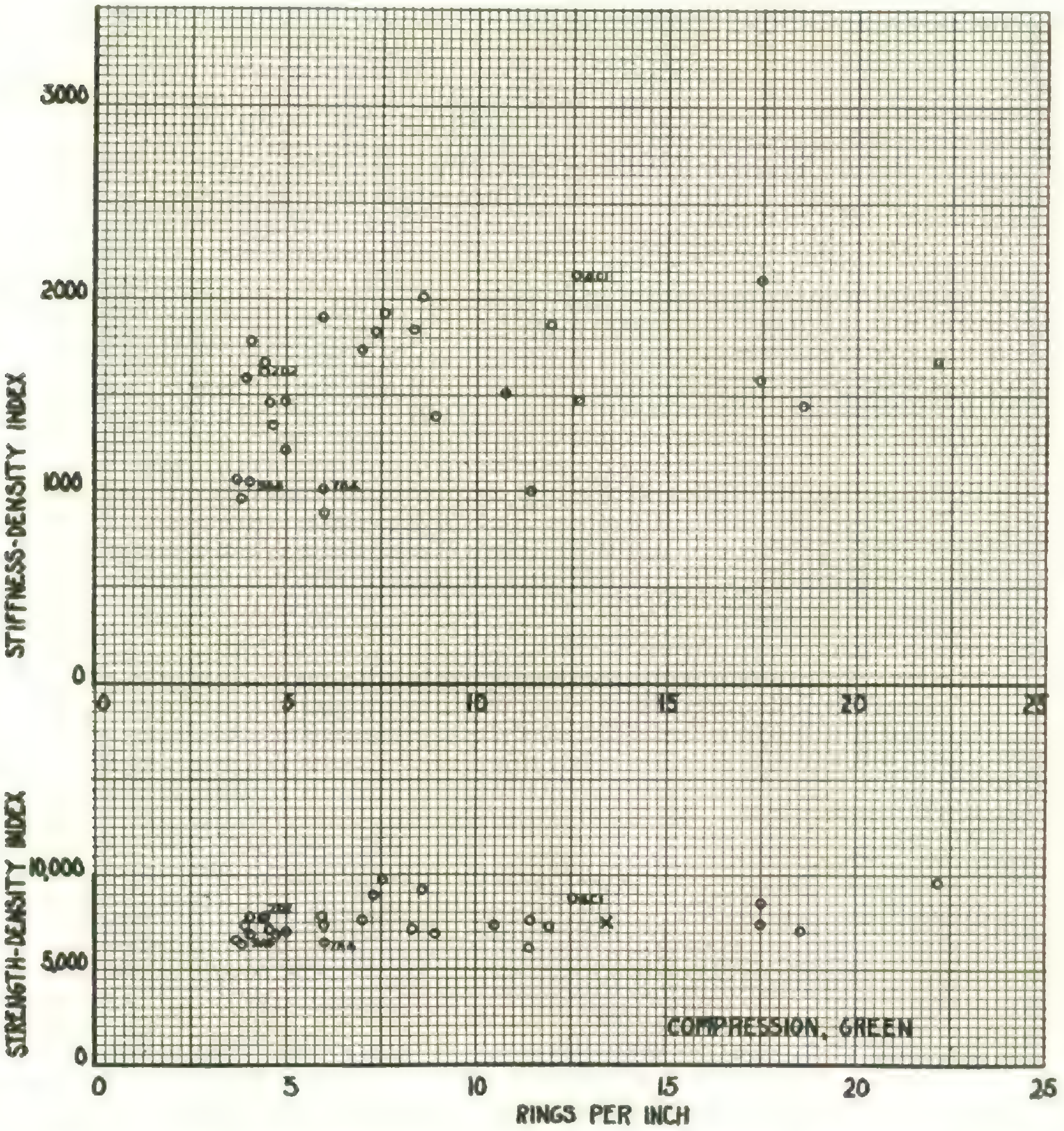

Fig. 6. Axial compression strength-density index (ultimate strength ÷ specific gravity) and stiffness-density index (modulus of elasticity ÷ specific gravity) plotted over growth rate for green specimens. X indicates strength-density index of average test for *Pinus echinata* from Arkansas (Markwardt and Wilson, '35).

wood,'' the present randomly selected groups of specimens were examined to show the effect on strength of this measurable feature of cell-wall structure. This relationship for compression strength, bending strength, and stiffness has been treated briefly by Pillow and Luxford ('37) and reviewed earlier in this paper.

Fairly simplified technique had to be developed to obtain representative averages for the comparatively large amount of material involved in this study. Sampling was done in the following manner. Blocks of material from the test specimens were cloven radially. Under the proper lighting angle there

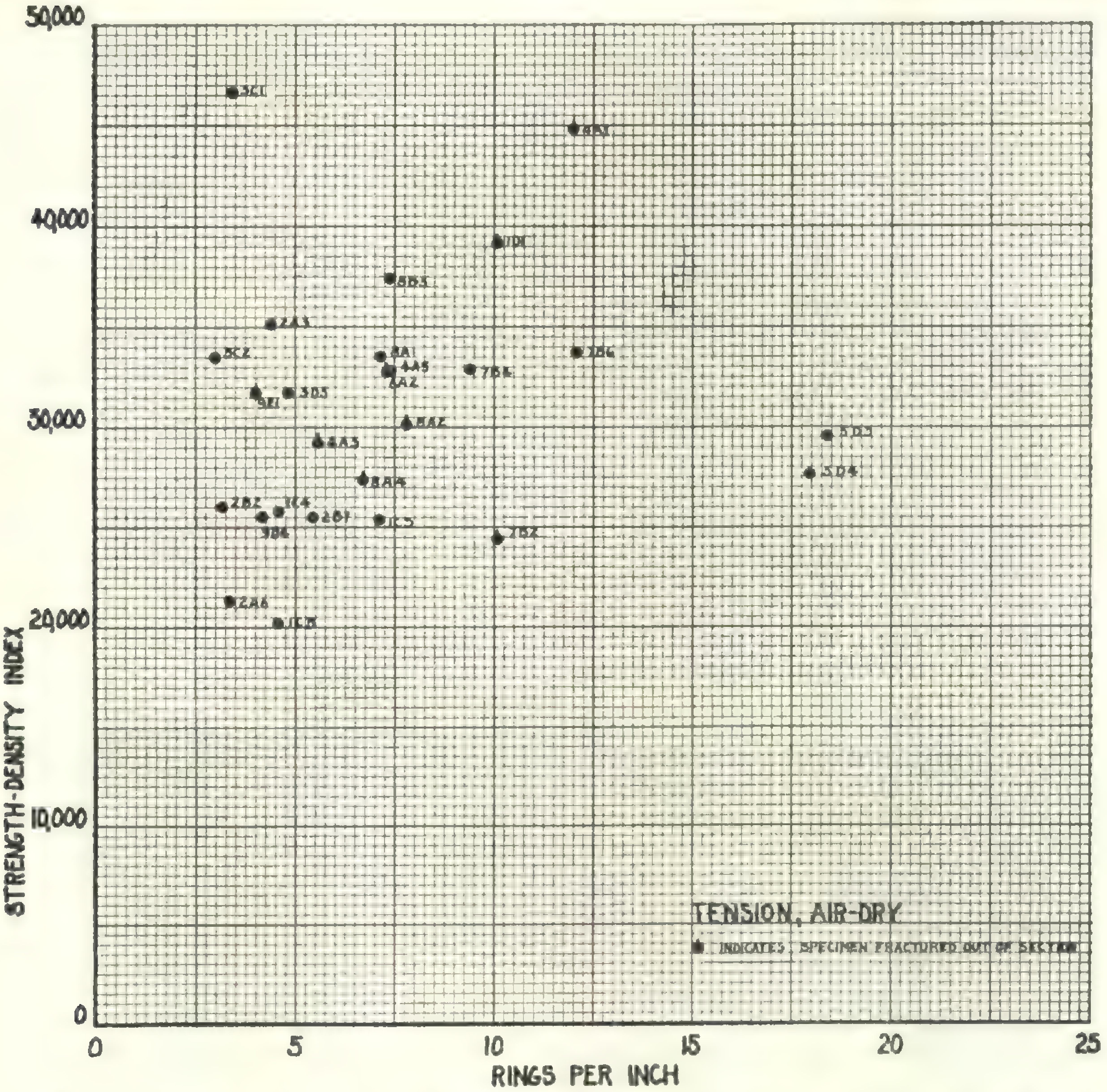

Fig. 7. Axial tension strength-density index (ultimate strength ÷ specific gravity) plotted over growth rate for air-dry specimens.

could be seen on the faces of the split halves small radial groups of fibers, often one cell thick, whose ends had been loosened from the wood. These one-celled rows were carefully cut free with a micro-knife and placed in benzol. When the benzol had displaced the air in the cells these "sections" were put in temporary microscope slide mounts in ordinary rubber cement. The non-swelling medium was designed to prevent

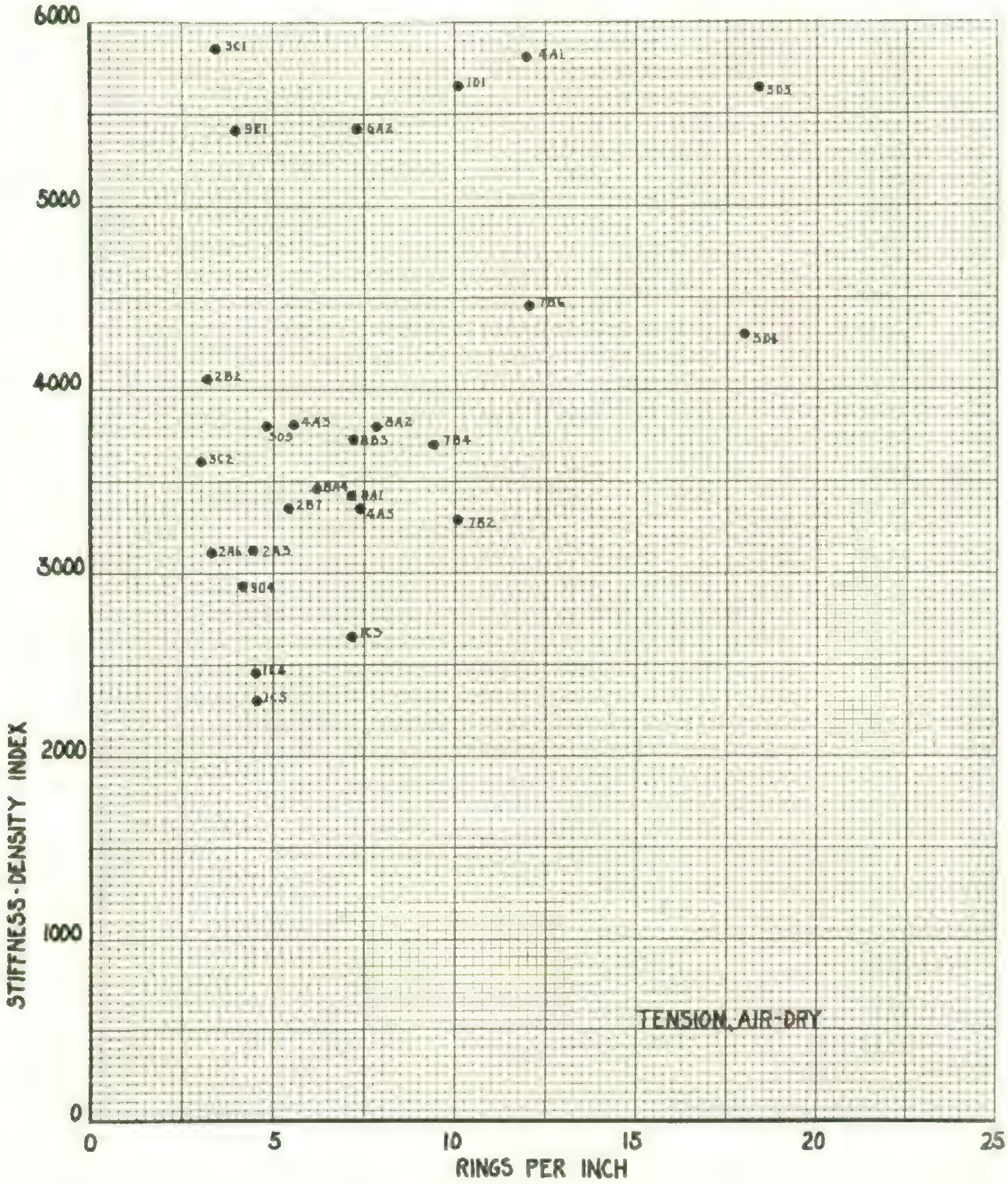

Fig. 8. Axial tension stiffness-density index (modulus of elasticity ÷ specific gravity) plotted over growth rate for air-dry specimens.

the disappearance of any fibrillar checks or striations occasioned by drying. The search for indication of slope of fibrils was made at 440 ×. Often the plane of orientation was indicated by cleavages in the central wall due to the splitting of

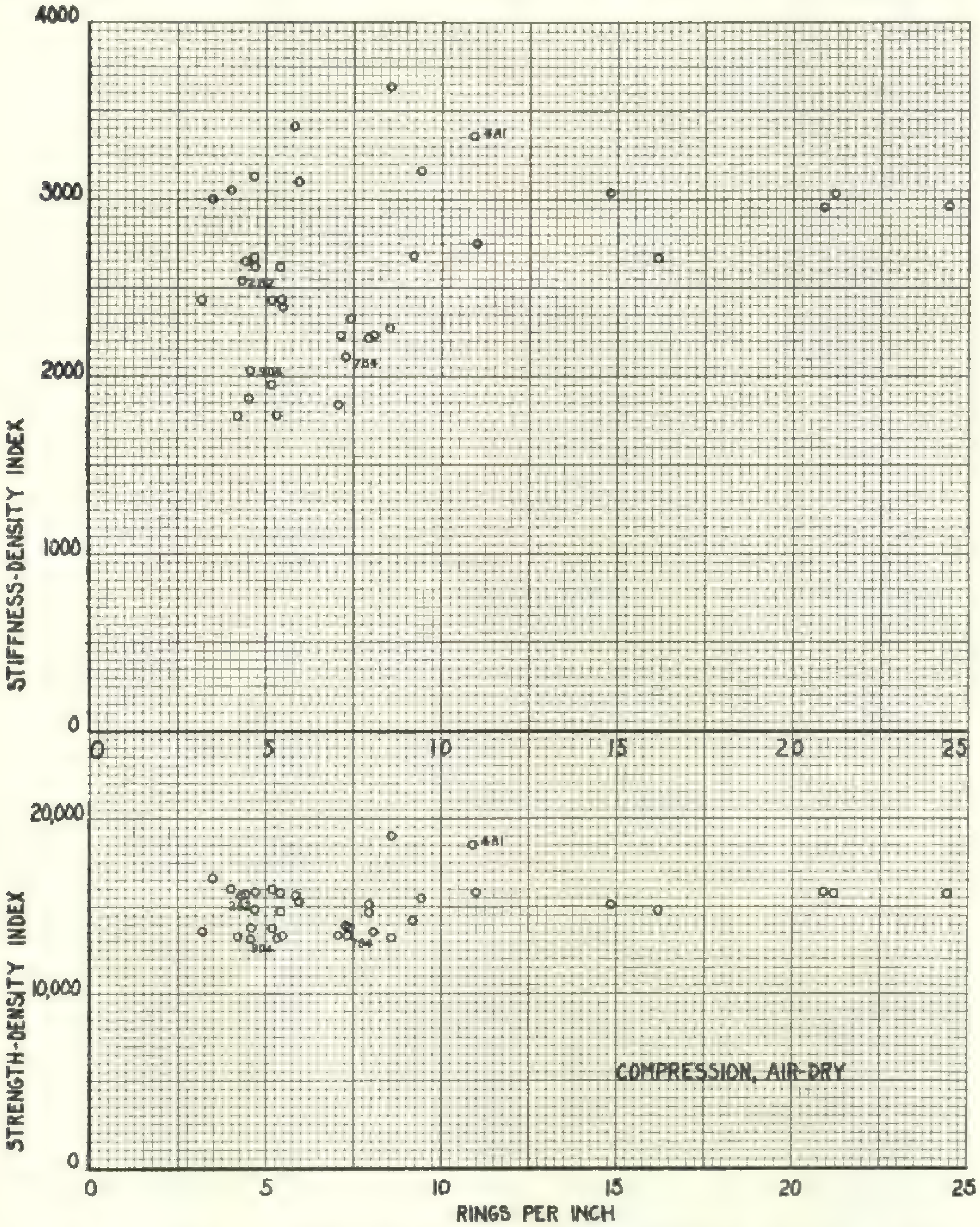

Fig. 9. Axial compression strength-density index (ultimate strength ÷ specific gravity) and stiffness-density index (modulus of elasticity ÷ specific gravity) plotted over growth rate for air-dry specimens.

the wood. Summerwood fibers of low angle were the most difficult, and often considerable searching for a single measurement was entailed. In difficult observations polarized light was employed to accentuate discontinuities and to check orientation angles.

Measurements were made by means of a cross-hair and a graduated revolving stage, and only in the clear, i.e., away from pits and rays. The average angle for each specimen is based on twenty measurements distributed as evenly as possible along the split radius according to the relative thickness of the summerwood. The tension specimens had more complete representation since they contained fewer growth rings. Many compression specimen rings were represented by a single measurement which was taken from about the middle of the summerwood.

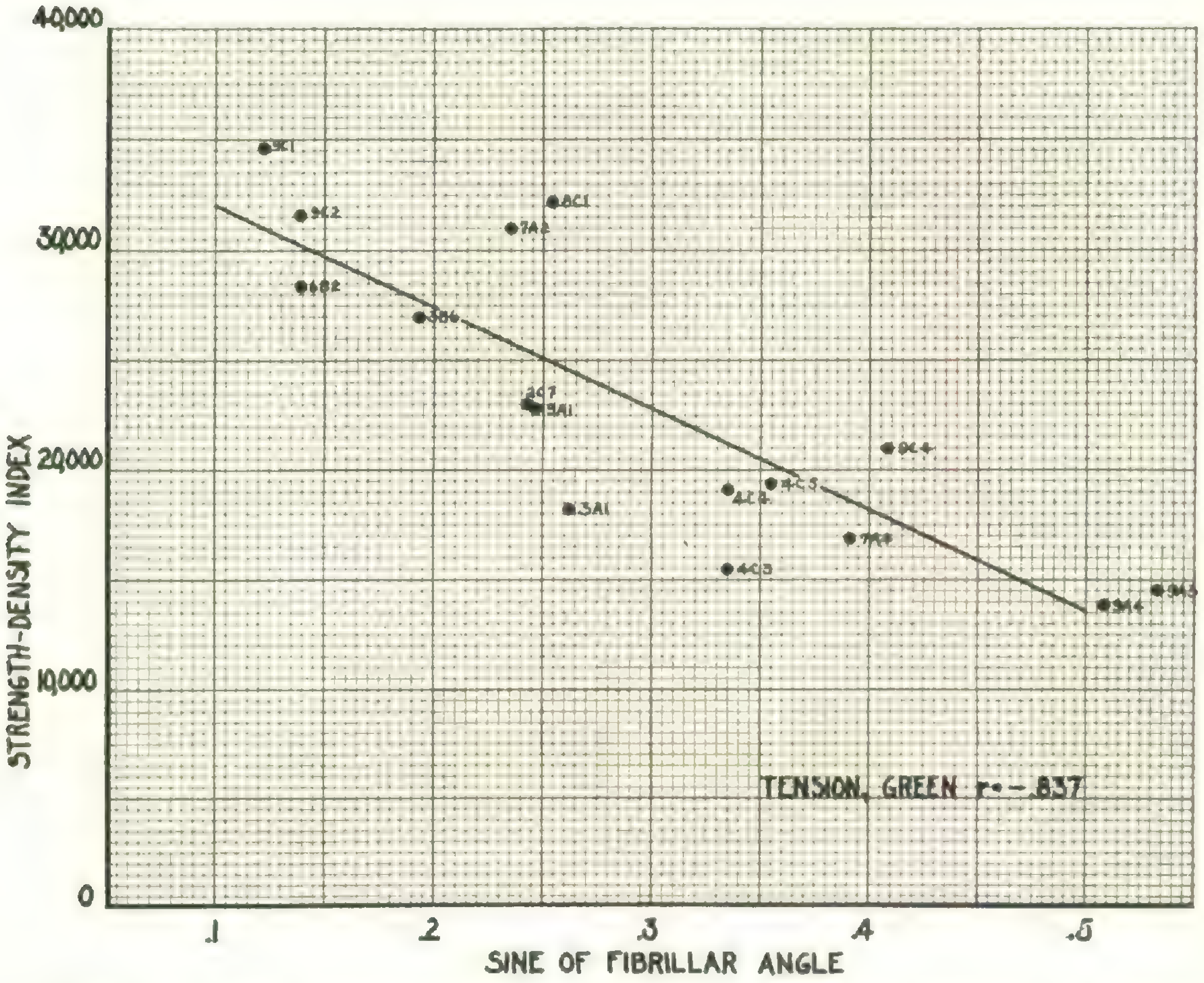

Fig. 10. Axial tension strength-density index (ultimate strength ÷ specific gravity) correlated with sine of average fibrillar angle in summerwood for green specimens.

For correlation purposes the fibrillar angle of summerwood only was measured. This deviates from the method of Pillow and Luxford ('37), who used an average angle "weighted on the basis of the proportions of springwood and summerwood and their respective slope." True representation of the wood for strength correlation requires weighting on the basis of

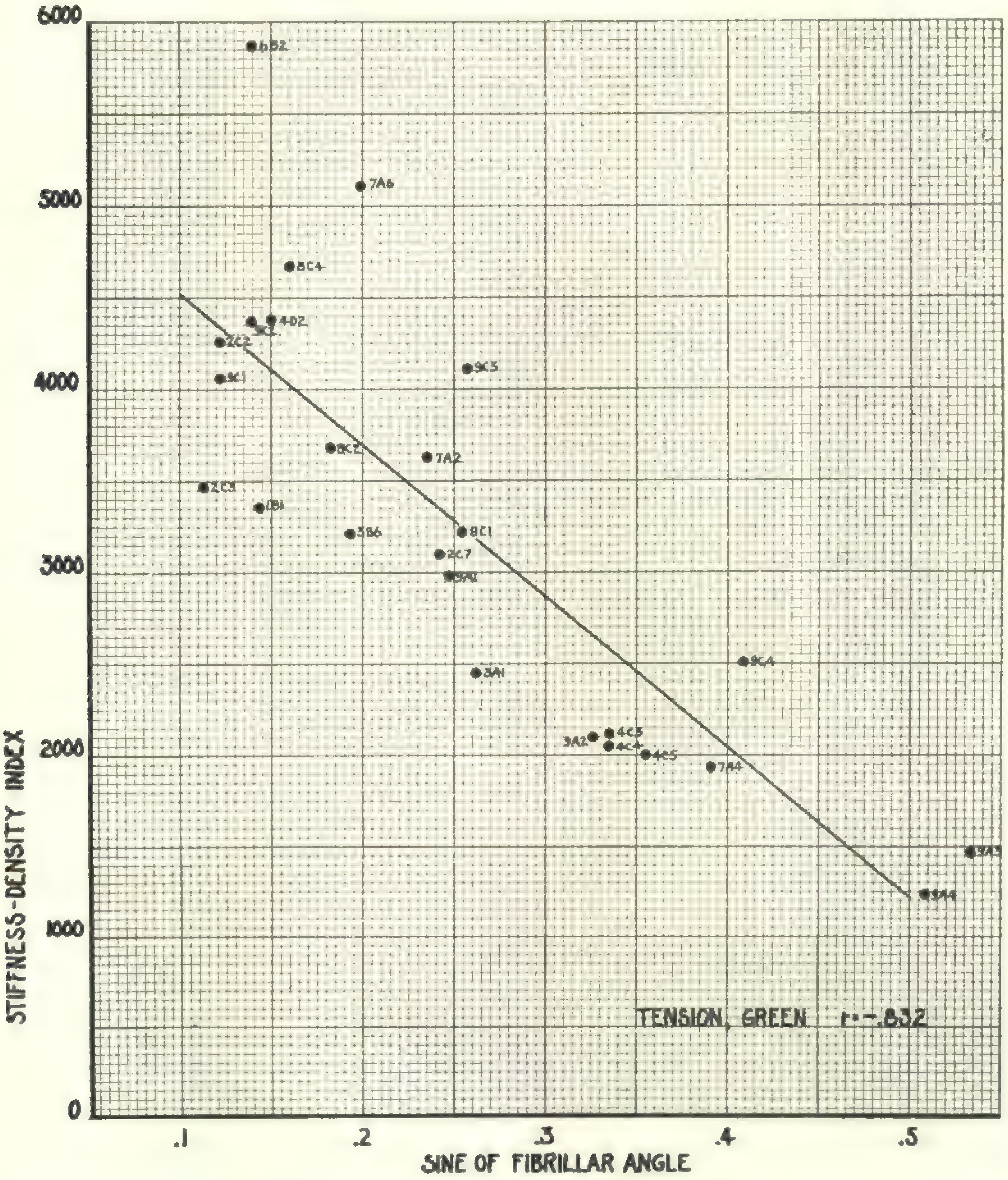

Fig. 11. Axial tension stiffness-density index (modulus of elasticity ÷ specific gravity) correlated with sine of average fibrillar angle in summerwood for green specimens.

weight. As a check on the validity of using only summerwood, twenty measurements each were made in the springwood of twelve tension specimens representing the complete range of angular variation. Averages of fibrillar angles were then calculated with weighting based on area proportion and specific gravity (constant weighting of three for summerwood and one for springwood, since Forsaith ('33) found approximately this relationship for southern yellow pine). These weighted averages were correlated with those for summerwood only, resulting in a correlation coefficient, r, of +.970, $t = 12.618$.

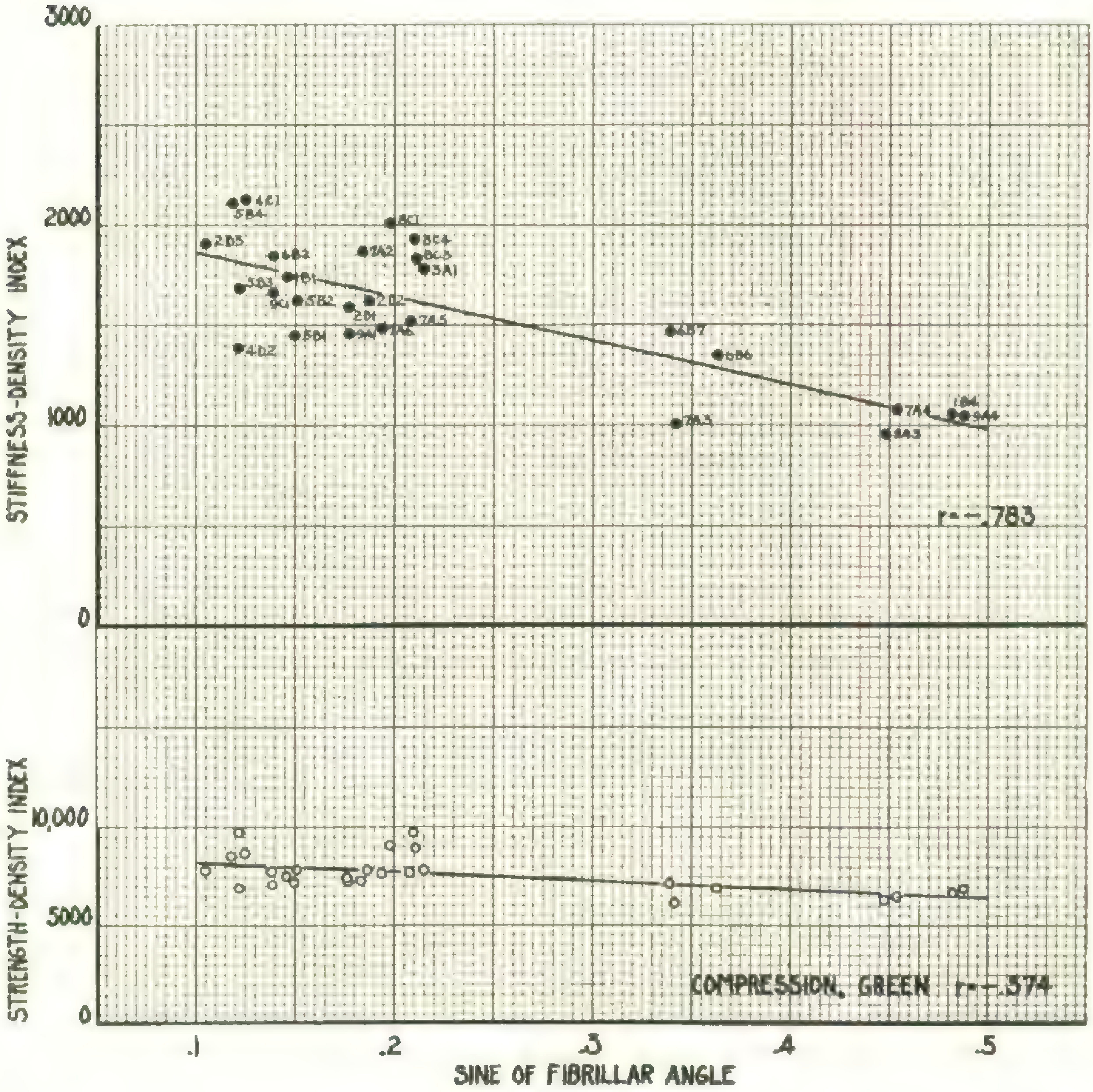

Fig. 12. Axial compression strength-density index (ultimate strength ÷ specific gravity) and stiffness-density index (modulus of elasticity ÷ specific gravity) correlated with sine of average fibrillar angle in summerwood for green specimens.

The average fibrillar angles of summerwood are given in column 11 of tables II to V, along with their sines. Graphical correlation of the sines with strength- and stiffness-density indexes for axial tension and axial compression in green and air-dry wood is shown in figs. 10 to 15. The product-moment regression line is superimposed on each chart. A summary of the product moment correlation coefficients and their reliabilities is given in table VI. All of the correlation coefficients are significant under the *t* test except that for dry tension strength-density, for which the probability of *r* being unrepresentative is slightly greater than 0.1. Unfortunately many of the

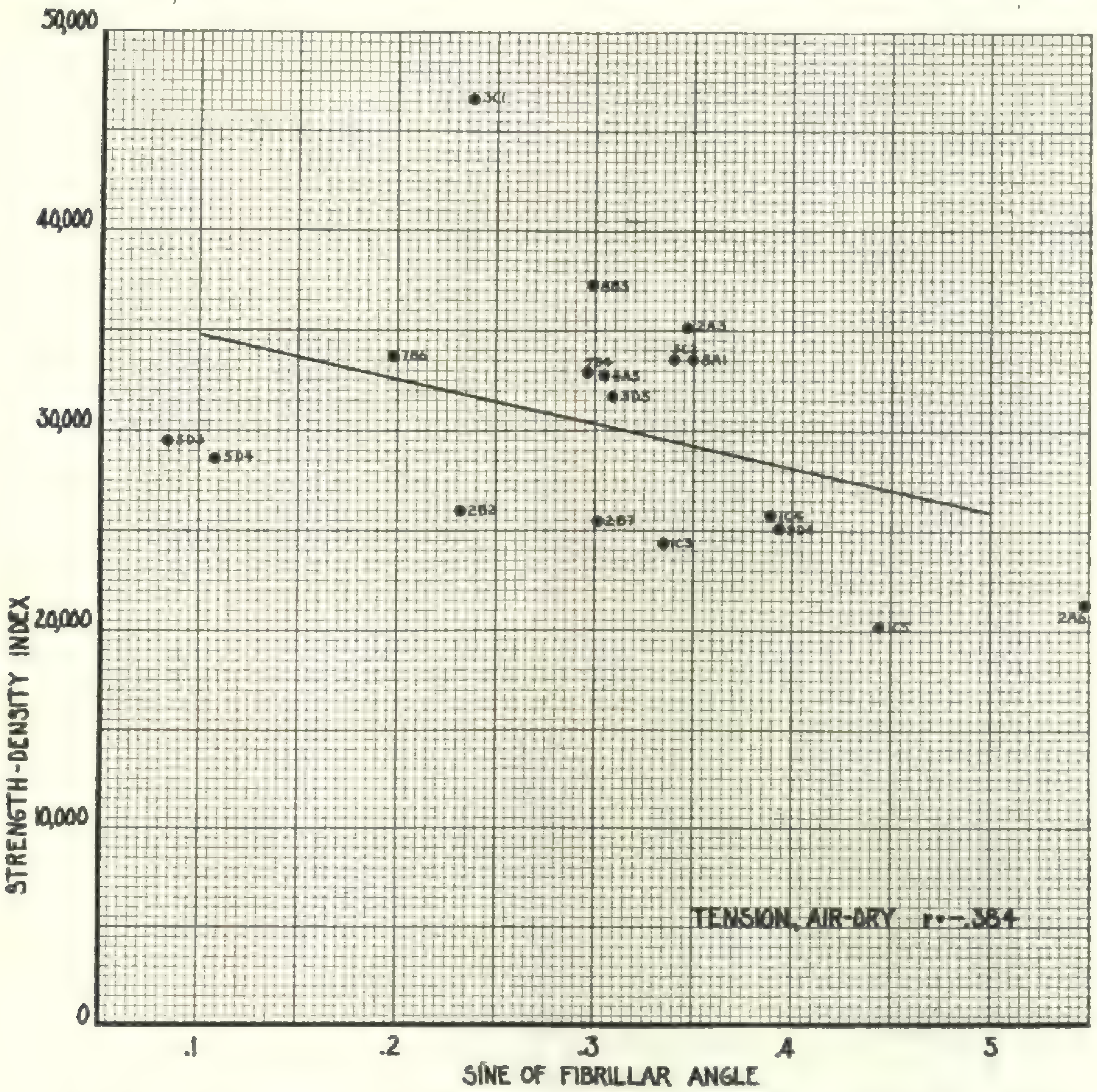

Fig. 13. Axial tension strength-density index (ultimate strength ÷ specific gravity) correlated with sine of average fibrillar angle in summerwood for air-dry specimens.

stronger specimens in this series failed to break in the test section and could not be used as reliable.

There appears to be little doubt but that the angle of fibrillar orientation or some factor closely associated with it is effective in determining the resistance of the wood to axial stresses. Whether the relationship in all series actually conforms to a

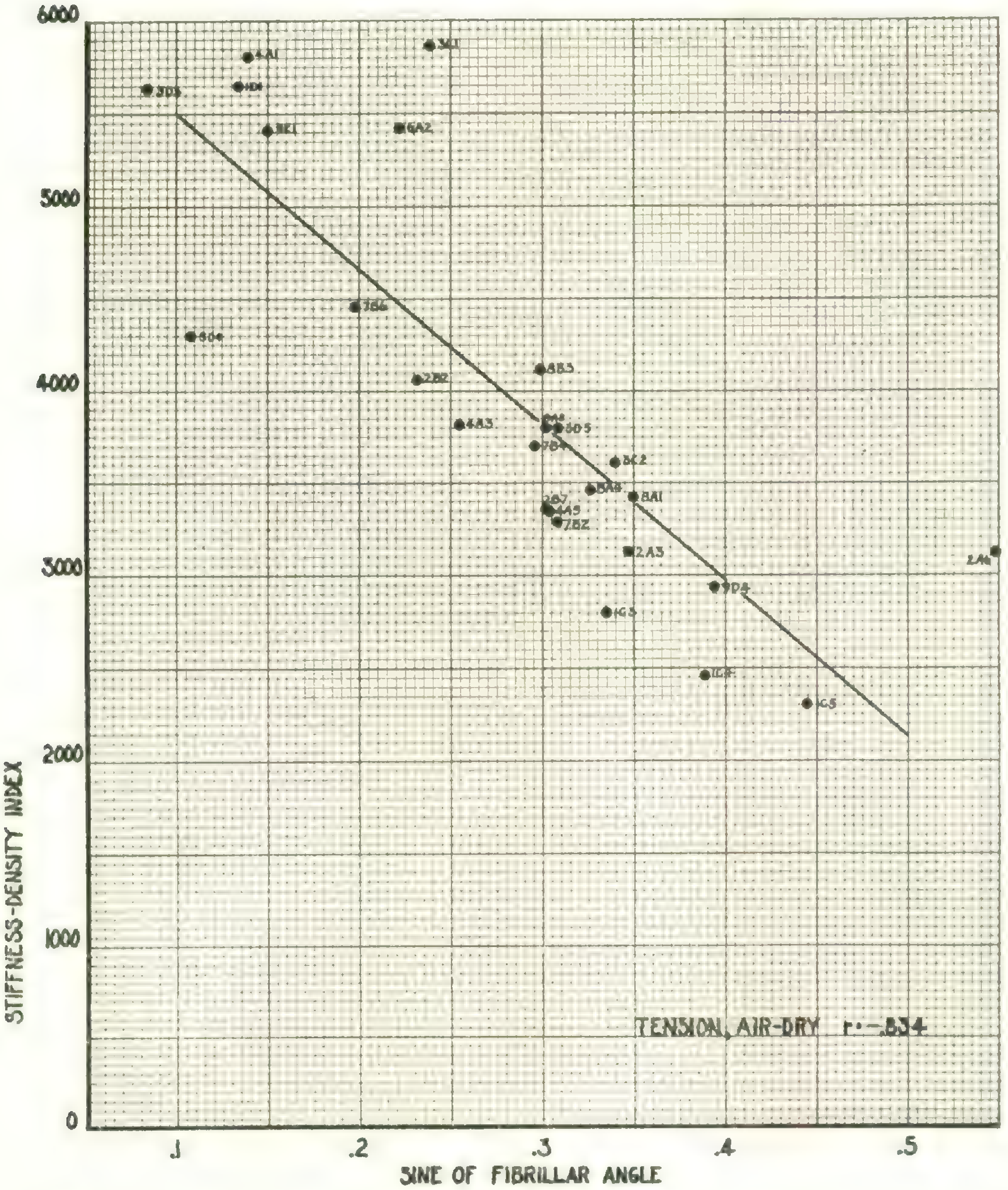

Fig. 14. Axial tension stiffness-density index (modulus of elasticity ÷ specific gravity) correlated with sine of average fibrillar angle in summerwood for air-dry specimens.

straight line may not be determined by the amount and distribution of the data at hand, though any curvilinearity in compression relationships would seem to be slight.

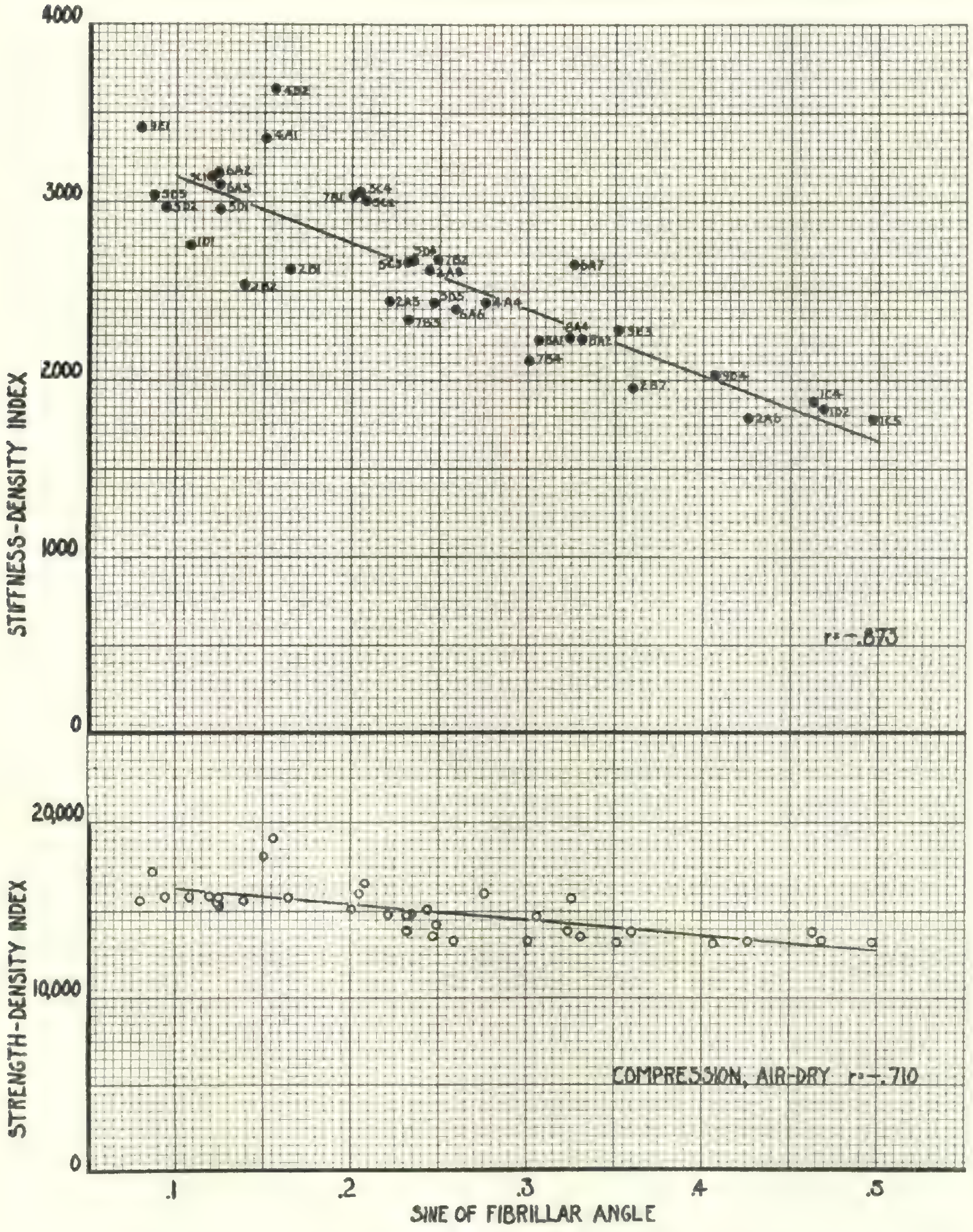

Fig. 15. Axial compression strength-density index (ultimate strength ÷ specific gravity) and stiffness-density index (modulus of elasticity ÷ specific gravity) correlated with sine of average fibrillar angle in summerwood for air-dry specimens.

TABLE VI

CORRELATION COEFFICIENTS OF RELATIONSHIPS OF STRENGTH- AND STIFFNESS-DENSITY INDEXES WITH AVERAGE ANGLE OF FIBRILLAR ORIENTATION IN SUMMERWOOD

Stress	Index	r	t
Green tension	Stiffness-density	−.832	7.192
Green tension	Strength-density	−.837	5.723
Green compression	Stiffness-density	−.783	6.294
Green compression	Strength-density	−.574	3.505
Dry tension	Stiffness-density	−.834	7.404
Dry tension	Strength-density	−.384	1.664
Dry compression	Stiffness-density	−.873	10.438
Dry compression	Strength-density	−.710	5.879

At least we have here the only yet known measurable criterion of the strength of wood substance, and its control in the investigation of any other factor is indicated as necessary.

The following observations on fibrillar orientation may be made from a study of the charts:

(1) The effect on tension strength and stiffness is greater than upon compression strength and stiffness.

(2) The effect on stiffness is greater than upon strength for both tension and compression.

(3) Drying increases the effect upon compression strength and stiffness, i.e., drying increases the compression strength and stiffness more in the specimens of low angle than in those of high angle.

(4) There appears to be more variability in specimens of low angle than in those of high angle.

(5) Support is given to the view that the fibers of "compression wood" have a structure that is merely an extreme case of a condition that occurs in all conifer tracheids and that "abnormality" in the strength properties of wood substance is quantitative rather than qualitative.

When the angular measurements were made, note was taken of the occurrence of checks in the central layer typical of "compression wood." There was no evidence to show that checks were associated with a constant limit in fibrillar angle, nor that their presence explained the variation of any of the strength properties at any given fibrillar angle. Checks were

noted with angles as low as 15° but many fibers with angles as high as 28° were found to be unchecked. Generally tension specimens exhibited checks at a slightly lower fibrillar angle than compression specimens.

Re-examination of growth rate as a factor showed that it is not responsible for the deviations still remaining in the correlation. The average ring width for specimens below the regression line is in none of the series significantly different from the average for specimens above the line.

The plotting in these charts serves as reference in a search for the remaining factors controlling the resistance of wood to longitudinal stress.

EXAMINATION OF TENSION FRACTURES OF THE WOOD

The fractured portions of the tension specimens were sawn out and carefully preserved for examination under a 42.5 × (supplemented by 130 ×) binocular microscope. Mounting the blocks on a universally movable holder enabled adjustment for the best possible light incidence on the fibers so that the relation of fiber fracture to wood fracture could be studied.

Generally brash failure for weak specimens and splintering for strong ones were noted. Green specimens splintered more than dry ones. Many strong dry specimens appeared to the eye to have brash failure but magnification showed the fracture to be composed of a large number of minute splinters of single fibers or small groups. Typical brash failure of weak wood exhibited the plane of fracture extending transversely across large groups of cells. Springwood portions were normally brash and summerwood splintered.

Cell end fracture appeared mostly transverse in summerwood fibers of strong pieces and frayed or spirally torn in those of weak ones. Springwood fiber end fracture was irregular, mostly with its general plane coinciding with the plane of failure of the wood.

Commonly fiber fracture was observed to coincide with edges of wood rays in summerwood, the cells being broken off in radial rows. This ray association was less regular in springwood. Very strong summerwood fibers fractured independ-

ently, and the point of fracture of very weak ones was determined by the general plane of fracture of the wood (brash fracture). Some summerwood fibers not fractured but with intact ends projecting were commonly found at the fracture of very strong dry specimens. In the green series a few of these fibers were usually found even in the weakest specimens.

Longitudinal cleavage of the wood (corollary to splintering) was most profuse in strong and green specimens. Gross tangential longitudinal cleavage was not confined to either type of tissue, and often the cleavage plane was observed to extend across the border between springwood and summerwood without interruption. Commonly the lateral fracture occurred through the cell in springwood and apparently between fibers in summerwood. Exceptions to this rule were observed in the occasional occurrence of torn summerwood lateral walls in weak dry specimens and the frequent untorn springwood lateral walls of strong green specimens. Where the walls appeared untorn in lateral separation, fragments of the outer layer of the secondary wall were frequently seen clinging to the cells. On flat planes there were areas where longitudinal plates of the outer layer (with middle lamella and primary walls between) had been pulled laterally from between the fibers on the opposite face of the plane. It was also frequently observed that the outer layer had been pulled from the central layer in transverse strips (according to the orientation of the cellulose in the outer layer). This separation of fibers at the interface between outer and central layer of the secondary wall was confirmed in the study of macerated fibers (pl. 3, figs. 1 and 3).

The implication from the more frequent occurrence of unfractured cells (central layer) in the green condition is that drying tightens the bond between outer and central layer, increasing the strain on the central layer and causing cell fracture rather than cell separation.

No constant criteria were derived from this study for the explanation of differences in strength between specimens of the same average angle of fibrillar orientation, though some

of the stronger specimens in the high-angle range exhibited the strong type of fracture (splinter) and some of the weaker specimens in the low-angle range tended to exhibit the weak type of fracture (brash). Weak green tension specimens 9-C-4 and 9-A-3 (figs. 4 and 5) did not have brash summerwood fractures and had some unfractured fibers projected at the wood fracture. Strong dry tension specimens 5-D-3 and 5-D-4 (figs. 7 and 8) were brash.

MICROSCOPIC EXAMINATION OF FIBERS

For studying the relation of failure to fiber structure a method of microscopic preparation was sought which would give most clearly the actual picture of conditions at the time of fracture. Isolation of fibers, under a dissecting microscope, with the aid of chemical maceration was chosen for this end. Short splinters were carefully split from fractured areas, boiled for several minutes (being held in water with a wire clamp), and treated with Jeffrey's macerating fluid (equal parts of 10 per cent chromic acid and 10 per cent nitric acid) until several radial layers of fibers were loose enough to be removed by means of chisel-pointed needles. These radial groups and some single fibers, after washing, were lifted on a needle from the water by surface tension and mounted on a microscope slide in glycerine jelly. No stain was used since it might have clouded the structural features that were deemed important in this study. A polarizing microscope was used to identify structural detail and to accentuate fracture planes.

Tension fiber fracture.—Springwood tracheids had fractured in no definable pattern (pl. 4, fig. 6), just as was noted in the low-power examination. The fracture often resembled that of a glass tube or, in the case of thicker walled-cells, the plane of fracture occasionally followed the fibril slope on one side of the cell and gave an irregular saw-toothed edge on the other. Ordinarily the fracture line avoided bordered pits but sometimes passed around the border. Infrequently the wall was torn at a pit, revealing an annular disc of outer layer which was shown from dissection and from birefringent properties

to have concentric fibrillar structure. In some springwood tracheids where fibrillar striations were apparent the lines were seen to fade out over the pit chamber, suggesting an especially closely knit structure of the central layer.

Summerwood fibers of steep fibrillar orientation typically had transverse fracture (pl. 3, figs. 1 and 3). The fracture within the central layer often had a "pipe-organ" pattern, i.e., fibrils or blocks of fibrils projected at uneven distances indicating both concentric and radial cleavage. In some steep-fibrilled specimens of relatively low strength (5-D-3 and 5-D-4) transverse cell fracture commonly sloped across the wall conforming to the slip lines seen in compression failure. Summerwood fibers of high fibrillar angle were commonly fractured along the fibril spiral with secondary planes at irregular angles (pl. 4, fig. 5), but some stronger specimens in this group (pl. 3, fig. 4), as well as those of medium fibrillar angle, exhibited various combinations of spiral and transverse fracture. In this medium fibrillar angle range there was some evidence that the stronger specimens exhibit transverse and "pipe-organ" fiber fracture (pl. 4, fig. 4).

In those cases mentioned in the previous section where summerwood fibers were not broken in the tension fracture of the wood but were slipped apart longitudinally, the plane of fracture was located between the outer and central layers rather than at the middle lamella. Figure 1 of pl. 4 shows some of these apparently unbroken fiber ends from which the outer layer has been slipped. A remnant of outer layer can be seen on the second fiber from the right. Figures 2 and 3 of pl. 4 show a complementary condition where the outer layers which have been pulled off are clinging to whole fiber ends. Figure 3 identifies the outer layer by its weak birefringence.

Lateral separation of fibers at the interface between outer and central layer is demonstrated similarly in pl. 3, figs. 1, 2, and 3.

Compression test fiber fracture.—Compression failure in springwood tracheids appeared as transverse undulating wrinkles in the double walls of adjacent cells without separa-

tion of the cells except at the region of gross fracture. With favorable position of the tracheids in the mount, slip lines were visible at the wrinkles. Some slip lines appeared in summerwood fibers in areas away from the gross fracture with no apparent distortion of the cell wall. At the region of gross fracture the fibers were usually bent in a reverse curve yielding to the diagonal shear plane in the wood, and they were separated at their radial sides. Often these bands appeared to be accentuations of natural bends in the wall at ray crossings (pl. 5, fig. 4) but this was not general. Slip lines were concentrated at the bends.

There appears to be little doubt but that slip lines are actually planes of shear in the central wall. Frequently an offset in the entire wall was seen to be associated with a slip line (pl. 5, fig. 4, upper right, and pl. 6, figs. 1 and 3, lower center). Sometimes bulges on the inner side of a wall were subtended by a pair of slip lines (pl. 5, figs. 1 and 2, upper right). Slip lines were less numerous and less prominent in the fractures of fibers of high fibrillar angle (pl. 6, figs. 5 and 6, pl. 7, fig. 4) where most of the displacement appeared to occur along fibrillar angle planes.

The angle of slip lines with reference to fiber axis had been given in the literature as about 70 degrees. This was observed in the present study to be a good figure for summerwood of "normal" wood, but aside from considerable variations in a single fiber there appeared to be variations in average angle between specimens. Table VII gives some examples of average slip line angles based on small samples.

TABLE VII

AVERAGE ANGLE (AND RANGE) OF SLIP LINES REFERRED TO THE LONGITUDINAL AXIS OF THE CELLS FOR COMPRESSION TESTS IN GREEN CONDITION (DEGREES)

	Low fibrillar angle		High fibrillar angle	
	4-C-1	2-D-2	9-A-4	7-B-4
Summerwood	(70) 72 (76)	(69) 72 (76)	(52) 58 (61)	(66) 68 (72)
Springwood	(52) 57 (62)	(48) 58 (63)	(40) 48 (60)	(41) 49 (59)

As in tension fracture, separation of the cells generally takes place at the interface between outer and central layer, with the middle lamella, primary walls and outer layers clinging to one of two separating cells. Plate 5, figs. 1 and 2, and pl. 6, figs. 1, 2 and 3 show remnants of outer layers that have been detached from adjacent cells. Plate 5, figs. 3 and 4, and pl. 6, fig. 4 show clearly the cleavage between central and outer layer. Because even the brief macerating treatment used here has caused some cell separation at the middle lamella it cannot be definitely stated that there is no mechanical cleavage at this plane. However, the evidence of mechanical cleavage between the layers of the secondary wall was so extensive as to give the impression that this point is normally the center of mechanical weakness between fibers.

In fibers of high fibrillar angle lateral fracture was sometimes not between the outer and central layer but within the central layer (pl. 7, figs. 1, 2 and 3). The central layer seems to be torn along fibrillar angle planes and in planes corresponding to slip lines.

A structural character not previously emphasized in descriptions of "compression wood" but found quite constant in specimens of high fibrillar angle is the thickness of the outer layer of the secondary wall. This outer layer was found to be relatively thick in summerwood fibers for these typically weak specimens. In fibers of medium and low fibrillar angle it varied considerably, and there was some evidence to indicate that thicker outer layers are associated with wood of low strength in its fibrillar angle class.

Figure 1 of pl. 8 shows a macerated fiber from dry tension specimen 1-C-3, a weak specimen of medium fibrillar angle. The outer layer can be plainly identified and appears in best focus on the upper wall at lower right. Figure 2 is the same view under polarized light, with the fiber at the position of maximum brightness. Here the outer layer is not visible since its fibrillar structure at the cell edges is parallel with the light axis. The reduction in apparent diameter of the fiber is partially accounted for by the thickness of the outer layer. The

magnification of the polarized-light pictures was reduced about 10 per cent by insertion of the analyzer. Figs. 3 and 4 are comparable views of a fiber from dry tension specimen 8-A-1, which has about the same average fibrillar angle as 1-C-3 but is much stronger. The two fibers have about the same total diameters in ordinary light but difference in outer layer thickness is shown by the difference in diameters under polarized light.

Specimen 1-C-3 is typical "compression wood" material, and the checks in the central layer which are visible may account for its strength deficiency as compared with specimen 8-A-1 in which checks were not found. Angle of fibrillar orientation, thickness of outer layer, and occurrence of fibrillar checks evidently vary independently.

With the interface between outer and central layer being definitely involved in separation of cells it might be questioned whether the fibrillar slope of the outer layer is important to strength. Very few fibers were found whose fibrillar orientation was not nearly transverse, and these were not confined to specimens of high or low strength.

The occurrence of slip lines appears to be an important influence upon tension strength. They were detected only in specimens which were weak for their fibrillar angles. Figures 5 and 6 of pl. 8 show a fiber from dry tension specimen 5-D-4 of low fibrillar angle and relatively low strength and stiffness in which typical compression slip lines can be faintly seen in the lower wall. End fracture of many fibers in this specimen conformed to these planes.

V. Discussion

The types of variations that may influence the axial strength properties of wood substance (strength of wood with density eliminated) may be enumerated as follows:

A. Architectural
   1. Growth rate
   2. Proportion of summerwood and springwood based on specific gravity

3. Tissue variation
4. Cell morphology

B. Constitutional
1. Cell-wall structure
2. Structure of the central layer
3. Distribution of constituents of the wood substance
4. Chemistry of constituents

This study has been concerned mainly with methods of fracture of a wood of simple anatomy with the aim of identifying the more important of the above variations. As a starting point the characteristics of "compression wood" have afforded clues for the solution of the problem, though no assumption has been made as to the relative importance of such characteristics or as to the interdependence of their variability.

Growth rate has long been associated with weakness in wood, and it still may be a good criterion for absolute strength. However, there is little indication that growth rate in itself has much influence upon the strength of wood substance. Figures 4 to 9 show that in both tension and compression many fast-grown specimens are strong for their density, and "abnormal" material is not excluded from narrower rings. Further, growth rate does not appear in this study to be associated with variations in the strength aside from those dependent upon the character of the cell wall (fibrillar angle).

Percentage of summerwood is an artificial criterion of absolute strength but has not been used in this study. It is recognized that the proportion of summerwood to springwood on the basis of solid volume may be important since it would reflect the relationship between average cell diameter and average cell-wall thickness in the two types of tissue.

In the wood under consideration histological variations appear to be minimized since one tissue preponderates. The variation in area of wood rays and resin ducts has been found by Berkley ('34) to be slight with reference to total sectional area and slight in average percentage between his strongest and weakest compression specimens "per unit weight." It

does not seem that the amount of ray tissue and area occupied by resin canals have considerable effect in determining axial strength properties though a variation in the number of rays may be important since they influence the morphology of tracheids.

Variations in the form of tracheids entail chiefly length, sectional shape and indentations caused by adjacent wood rays, and the occurrence of bordered pits. Since generally fiber fracture occurs in both tension and compression on transverse planes it is not thought that tracheid length is very important. It may influence the tensile strength of specimens in which many fibers are pulled apart longitudinally without fracture of the central layer. In these cases longitudinal shear is involved and the average shear area is less for shorter fibers. Berkley's ('34) outlying compression specimens were not significantly different in fiber length.

Variation of sectional shape from rectangular to circular, though it constitutes one difference between "normal" wood and "compression wood," has not been investigated. Mechanically the advantage in this respect for compression strength would seem to be on the side of the more cylindrical fibers of "compression wood."

The curves in tracheid walls at the edges of wood rays have often been seen in this study as points of fracture in both tension and compression though this is more general in tension fracture than in compression. Correlation of tensile strength with number of rays per unit area may be worthy of investigation since this is known to vary considerably within a tree.

Bordered pits have been proposed as sources of weakness in cell walls, but they rather seem to be in themselves sources of strength in tension. The possibility remains that a preponderance of bordered pits causes weakness because of the deviation of the fibrils of the central layer around them.

The detailed work recently published by Dr. I. W. Bailey and his associates on the constitution of the tracheid wall provides a basis for interpretation of mechanics of the failure of wood substance. The true middle lamella is a very thin

layer of isotropic material separating the cells. This binding material has been mentioned as having influence upon strength but it has been shown in this study as less apt to be a plane of weakness than structural planes within the wall itself. Actually under axial loads separation of cells is usually only incidental to yield within the cell wall. Under compression loads cells separate only when the walls have already failed in diagonal shear. In longitudinal tension, separation appears to be caused by lateral tension between cells resulting from lateral compression within a cell or group of cells, a component of the longitudinal tension force. Evidence of this is seen in the manner of fracture of sheets of double outer layers that obviously have been pulled laterally from between cells (pl. 3, fig. 3). In those cases where the central layer is not fractured in axial tension (pl. 4, fig. 1), failure occurs from longitudinal shear between outer and central layer. The lateral fracture within the central layer (pl. 7, figs. 1, 2 and 3) is interesting in view of findings of Bailey and Kerr ('37), that the two layers of the secondary wall in "Rotholz" tracheids are separated by "an isotropic layer of non-cellulosic composition." It would appear that the isotropic material is stronger in tension than is the cellulose structure perpendicular to its orientation plane.

The primary wall has not been identified with mechanical failure, and it is probable that it is so closely associated with the amorphous material of the middle lamella that it does not act independently.

Wide variation in the thickness of the outer layer of the secondary wall in summerwood leads to the conclusion that this may be an important measurable criterion for axial strength. The fibrils here approach transverse orientation and are at least an advantage in resistance to longitudinal or local shear stresses. Further, the peripheral position of the layer causes slight deviations in thickness to be reflected in disproportionate changes in sectional area of the cell wall. As an example, measurements from pl. 8, figs. 1 to 4 may be given. When diametrical measurements are made on the photographs (considering the difference in magnification between ordinary

and polarized light) and the circular areas of the layers computed, it is seen that the outer layer has 52 per cent of the total wall area in the fiber of 1-C-3 and only 26 per cent in the fiber of 8-A-1. The thicknesses of the outer layer indicated by this method of observation are 4.2 μ and 2.4 μ respectively. Because the sections of the fibers are not circular as has been assumed in this example and because of the possibility of optical error, this technique is not recommended for measuring the variable. However, justification for work on an accurate method of measurement in connection with strength studies is indicated.

That the characteristics of the central layer of the secondary wall are the most important criterion of axial mechanical properties of wood substance is suggested by the fact that variations in stiffness dependent upon fibrillar angle are greater than the remaining variations (figs. 10 to 15). This evidence is not seen in the consideration of ultimate strength, and it might be assumed that different factors affect stiffness and strength. It is more probable that the greater variation in ultimate strength is caused by uneven distribution of stresses and consequent local failure precipitating the failure of the specimen. Thus modulus of elasticity is probably the best measure of average mechanical resistance.

There appears to be some connection between the relationships of stiffness with fibrillar angle and what we now know of the structure of the cell wall and its method of fracture. Resistance in tension is about twice that in compression in fibers of steep angle. In this type of fiber, tension fracture has been shown to result from longitudinal strain on the elongated cellulose framework; the system is broken. Compression fracture in these fibers is a result of diagonal shear strain (along slip lines) across the concentric density laminae of the cellulose system. Actual rupture is not usually visible, and it is probable that there is involved only distortion, perhaps bending of fibrils similar to that in gross fracture.

Stiffness in tension is shown to be only slightly higher than that in compression in fibers of high fibrillar angle. Here both

tension and compression fracture are seen to result from shear strain between the fibrils or along the radio-helical discontinuities in the cellulose framework shown by Bailey and Kerr ('37) to occur in "compression wood." This is undoubtedly because the fibrillar angle approaches the theoretical 45° angle of shear which tends to operate under simple loading. An additional reason applicable to the compression mechanism is the radial density pattern in the central layer, providing resistance to shear across the wall.

Further evidence that the mechanism of resistance for compression is different from that of tension is seen by an examination of the effect of drying. Stiffness in tension is increased about the same amount throughout the range of fibrillar angle, which is only slightly less than the increase for compression stiffness at high fibrillar angles. At low angles for compression stiffness the increase is approximately doubled. It seems a logical conclusion that shear across fibrils (slip lines) is more concerned with secondary valences than is inter-fibrillar shear.

Since the transition from normal to "compression wood" is a gradual one, changes in fibrillar angle are perhaps more or less accompanied by changes in other characters, and it may not be stated positively that the dependence shown in these charts is attributable solely to the measured variable. However, this study indicates that some of the structural features of "compression wood" do not vary concurrently. Proportion of outer layer in the secondary wall and pattern of density variation in the central layer are two characters which are worthy of further investigation in a search for causes of variation from the relationships of axial strength to fibrillar angle. Quantitative criteria for the latter feature might be found in the angle of slip lines and the frequency of central wall checks. It may be discovered that the change from concentric to radial density pattern is a positive influence on compression strength since it tends to inhibit the formation of slip lines.

Koehler ('33) has stated that compression damage, sustained in the tree and indicated by slip lines, is a cause of brashness in tension. This seems to be confirmed in this study

where slip lines are associated with relatively low tension strength (pl. 8, figs. 5 and 6). There is a possibility that tension strength is affected by this factor without detection, i.e., the damage may be so slight that slip lines are invisible with technique now available.

Summary

The factors necessary of consideration in a complete study of the strength properties of coniferous wood are reviewed with stress upon the structure of the tracheid wall.

Four series of engineering strength tests are reported for carefully chosen specimens representing nine logs of commercial shortleaf pine wood; (1) axial tensile strength, green wood, (2) axial tensile strength, air-dry wood, (3) axial compression strength, green wood, (4) axial compression strength, air-dry wood. Ultimate strength and modulus of elasticity are given for each test. The factor, specific gravity, is eliminated from the comparisons of specimens by expressing mechanical properties as "strength-density index" (ultimate strength ÷ specific gravity), and "stiffness-density index" (modulus of elasticity ÷ specific gravity).

These indexes are plotted over growth rate, showing that this is not a universal criterion of mechanical properties of wood substance, though it controls the frequency of occurrence of weak specimens.

The indexes are correlated with the sine of the average angle of fibrillar orientation in summerwood, resulting in significant product-moment correlation coefficients in all cases except one in which the distribution of the data is obviously inadequate. Variations from the regression lines are not connected with growth rate.

Examination of tension fractures under low-power binocular microscope revealed the following:

(1) The typical brash gross failure observed for strong dry wood is not of the same cellular detail as that exhibited by weak specimens.

(2) Fracture of springwood cells is determined generally by the plane of shear stress for the wood.

(3) At longitudinal cleavage planes in summerwood, fragments of outer layer are seen clinging to apparently whole cells, indicating that cell separation may occur between outer and central layers of the secondary wall rather than at the middle lamella. Longitudinal cleavage in springwood is fracture through the cells.

(4) End fracture of radial rows of tracheids often occurs at the intersection of these cells with one edge of a wood ray.

(5) Some fibers, unfractured in tension, are seen in strong dry specimens and more widely distributed in the green series.

(6) There is some evidence that brash failure is associated with relatively low strength among specimens of steep fibrillar angle and that splintering occurs with relatively high strength at high fibrillar angles.

The principal observations in microscopic examination of isolated fibers of tension specimens are as follows:

(1) Bordered pits are not sources of weakness.

(2) Concentric arrangement of fibrils in the outer layer of the secondary wall at bordered pits is confirmed.

(3) Springwood cells generally fracture in no definable pattern.

(4) Fibers of steep fibrillar orientation have transverse fracture with some independent fracture of groups of fibrils; some of the weaker specimens have fiber fracture conforming to typical compression slip lines.

(5) Summerwood fibers of high fibrillar angle fail mostly along fibrillar planes with some secondary planes of irregular angle.

(6) Medium fibrillar angles are associated with various combinations of transverse and spiral fracture, with stronger fibers favoring the transverse type.

(7) Lateral separation of fibers is seen to occur mostly, if not always, at the interface between outer and central layers of the secondary wall.

(8) Where fibers are not fractured in tension, failure is indicated as longitudinal shear between outer and central layer.

The following observations concern fibers in compression specimens:

(1) Slip lines are confirmed as planes of shear on the cell wall.

(2) Fracture of fibers of steep fibril angle is seen as bending in the cell wall where slip lines are concentrated.

(3) Fiber fracture at high fibrillar angles follows fibrillar planes.

(4) Cell separation is normally between outer and central layers of the secondary wall.

(5) Cell separation in summerwood fibers of high fibrillar angle may occur within the central layer.

(6) There is some evidence that slip line angles are greater in material of low fibrillar angle.

Wide variation is shown to occur in thickness of outer layer, with greater thickness mostly associated with greater fibrillar angle.

The relative importance of the factors that may affect the axial strength properties of wood is discussed, and it is concluded that the factors most likely connected with variations remaining after control of specific gravity, moisture, and fibrillar angle are:

(1) Proportion of springwood and summerwood by weight.

(2) Proportion of outer layer to central layer of the secondary wall by sectional area.

(3) For compression strength—variation of angle of slip lines and frequency of fibrillar checks.

(4) For tension strength—number of wood rays per unit of tangential area.

(5) For tension strength—the degree of compression damage previously sustained as seen by the occurrence of slip lines.

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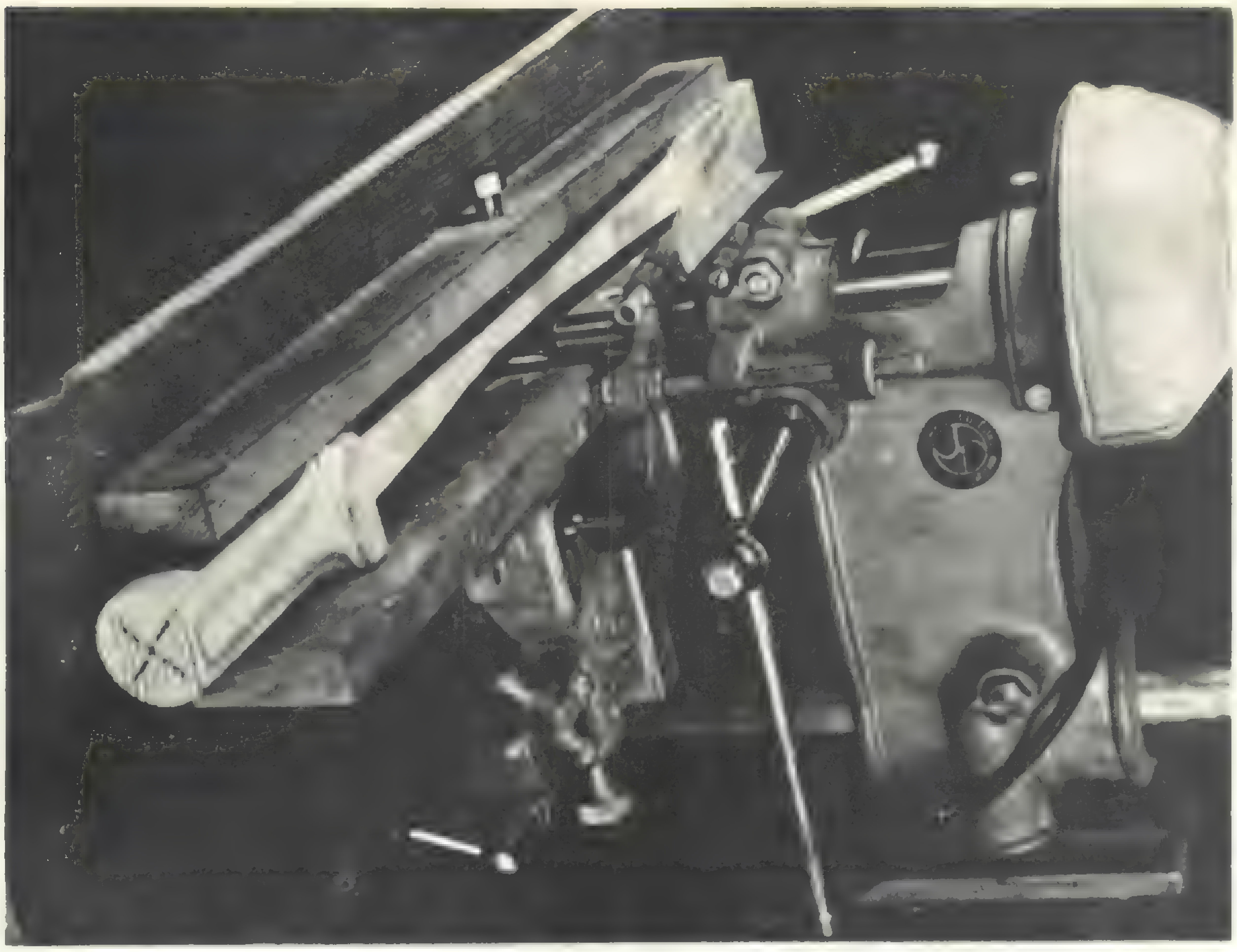
Explanation of Plate

PLATE 1

Fig. 1. Drill press with shaper arranged for finishing test sections of tension specimens.

Fig. 2. Tension specimen in Amsler hydraulic testing machine with extensometer in place.

[*Note.* An error has been made in labeling all of the accompanying plates Volume 27 instead of Volume 26.]



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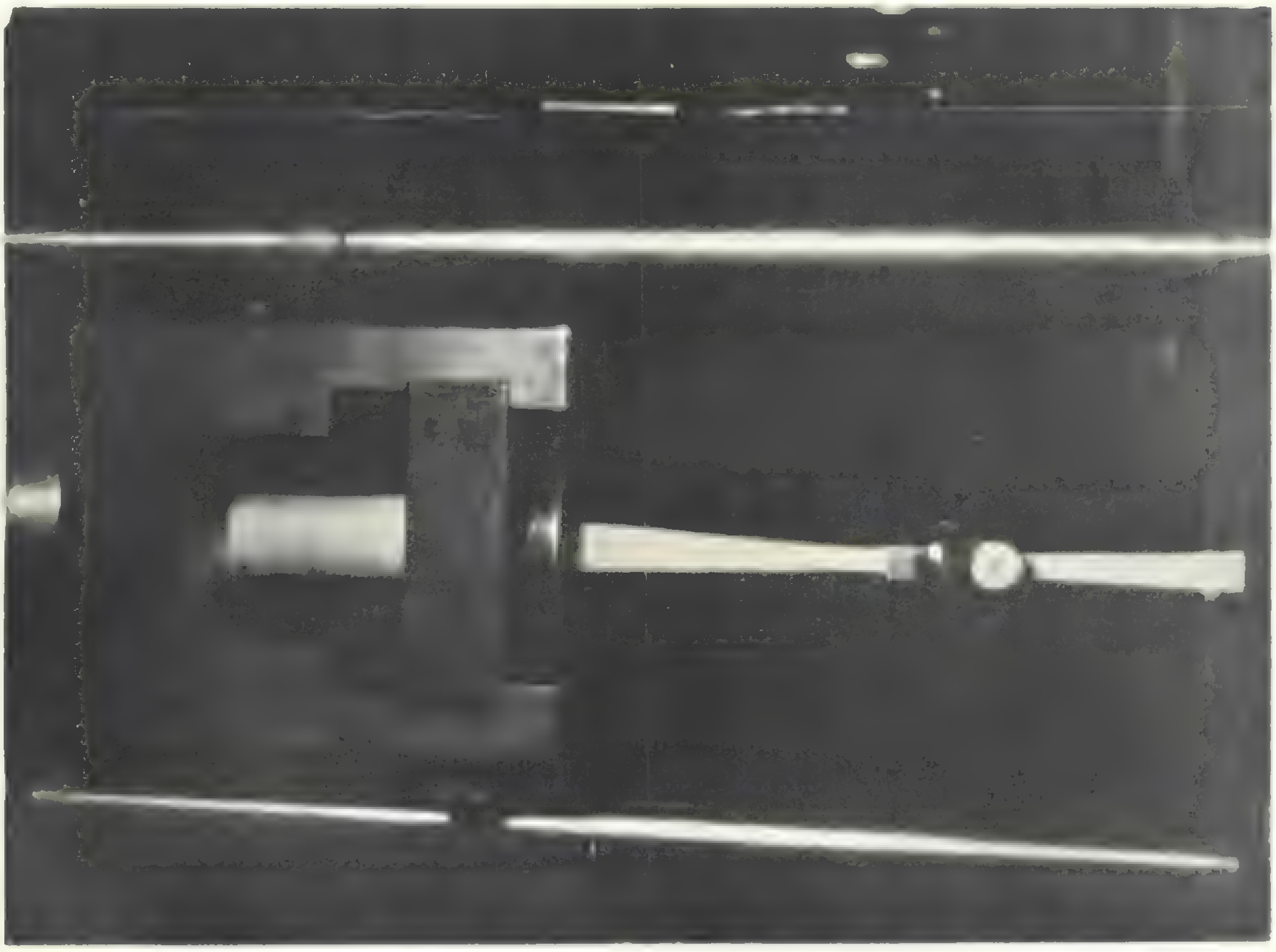


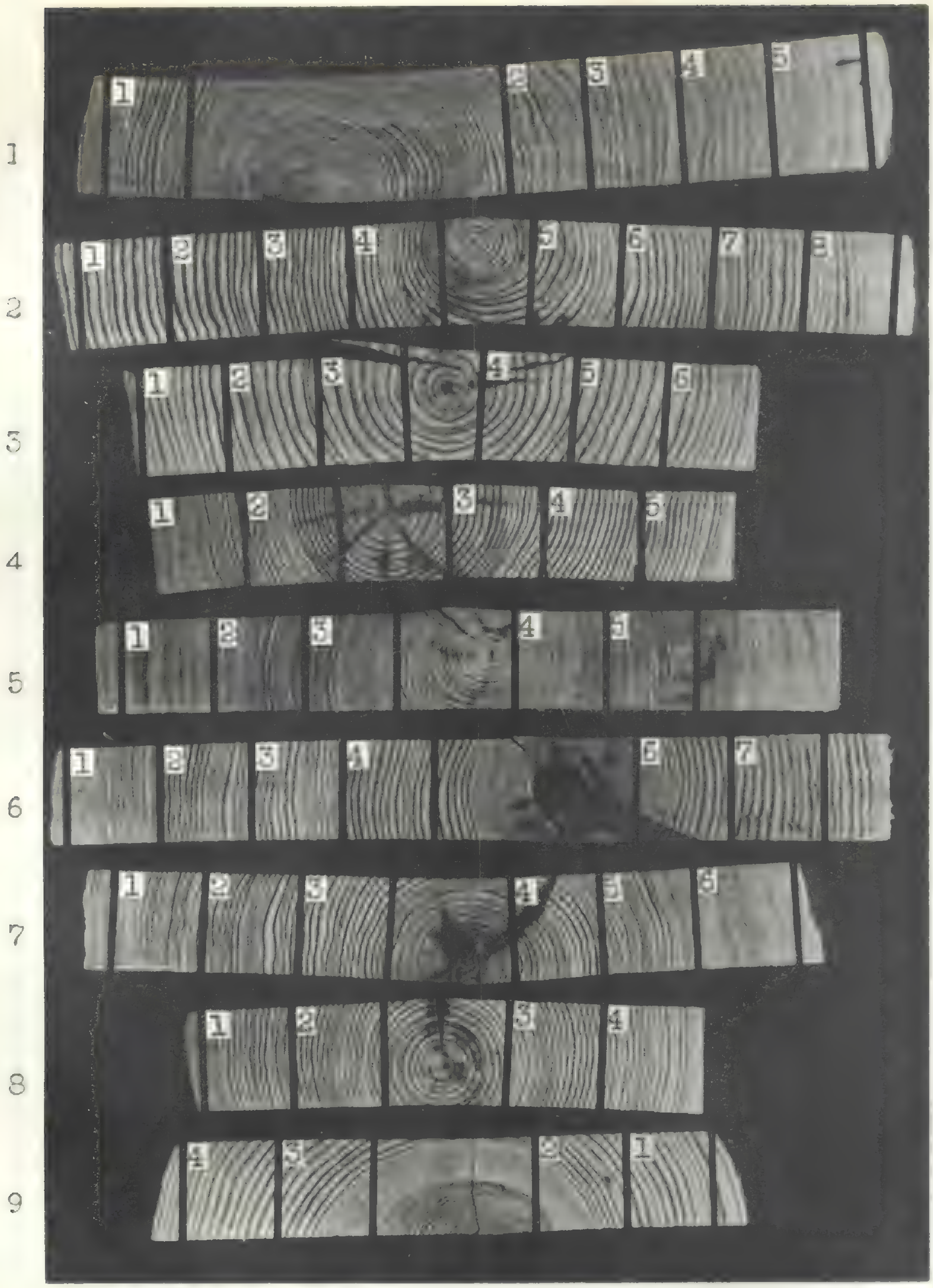
2

GARLAND—WOOD STRENGTH AND MICROSCOPIC STRUCTURE

Explanation of Plate

PLATE 2

Cross-section from the middle of the 2½-inch planks used for testing, with positions of specimens indicated.



GARLAND—WOOD STRENGTH AND MICROSCOPIC STRUCTURE

Explanation of Plate

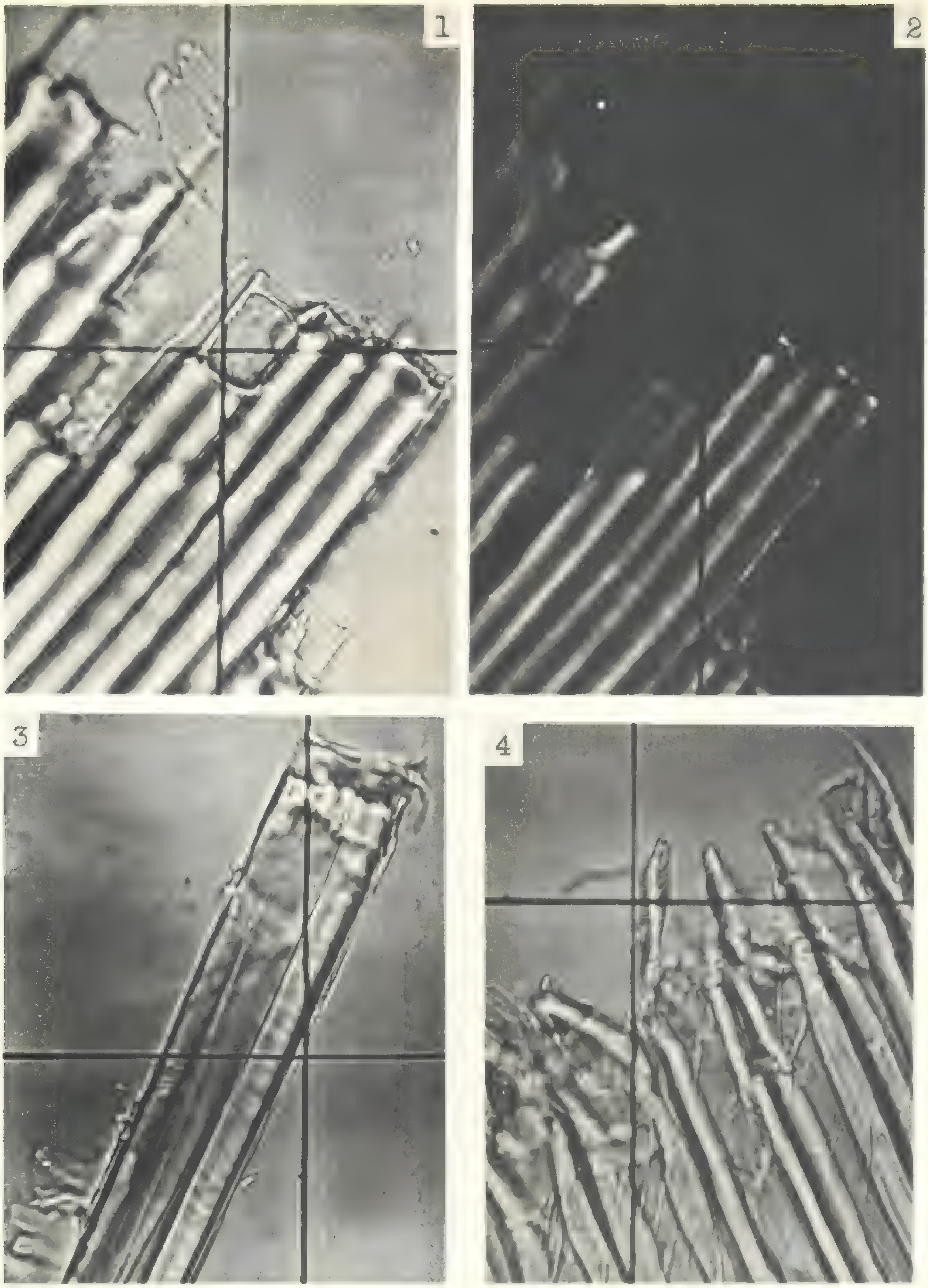
PLATE 3

Fig. 1. Radial group of summerwood tracheids from green tension specimen 8-C-4, showing typical transverse and ''pipe-organ'' fracture of strong fibers. Note sleeves of outer layer projecting. × 440.

Fig. 2. Same as fig. 1 with analyzer inserted. × 396.

Fig. 3. Summerwood tracheid from green tension specimen 2-C-2, showing typical end fracture of strong fibers and fracture of outer layer due to lateral separation. × 440.

Fig. 4. Radial group of summerwood tracheids from dry tension specimen 2-A-6, showing combination of spiral cleavage and transverse fracture. This specimen is relatively strong for its high fibrillar angle (sine, .550). × 440.



GARLAND—WOOD STRENGTH AND MICROSCOPIC STRUCTURE

Explanation of Plate

PLATE 4

Fig. 1. Radial group of summerwood tracheids from green tension specimen 9-C-1 at fracture, showing fiber ends whole, common in strong specimens. It is evident that these tips consist of a central layer from which the outer layer has been pulled. × 440.

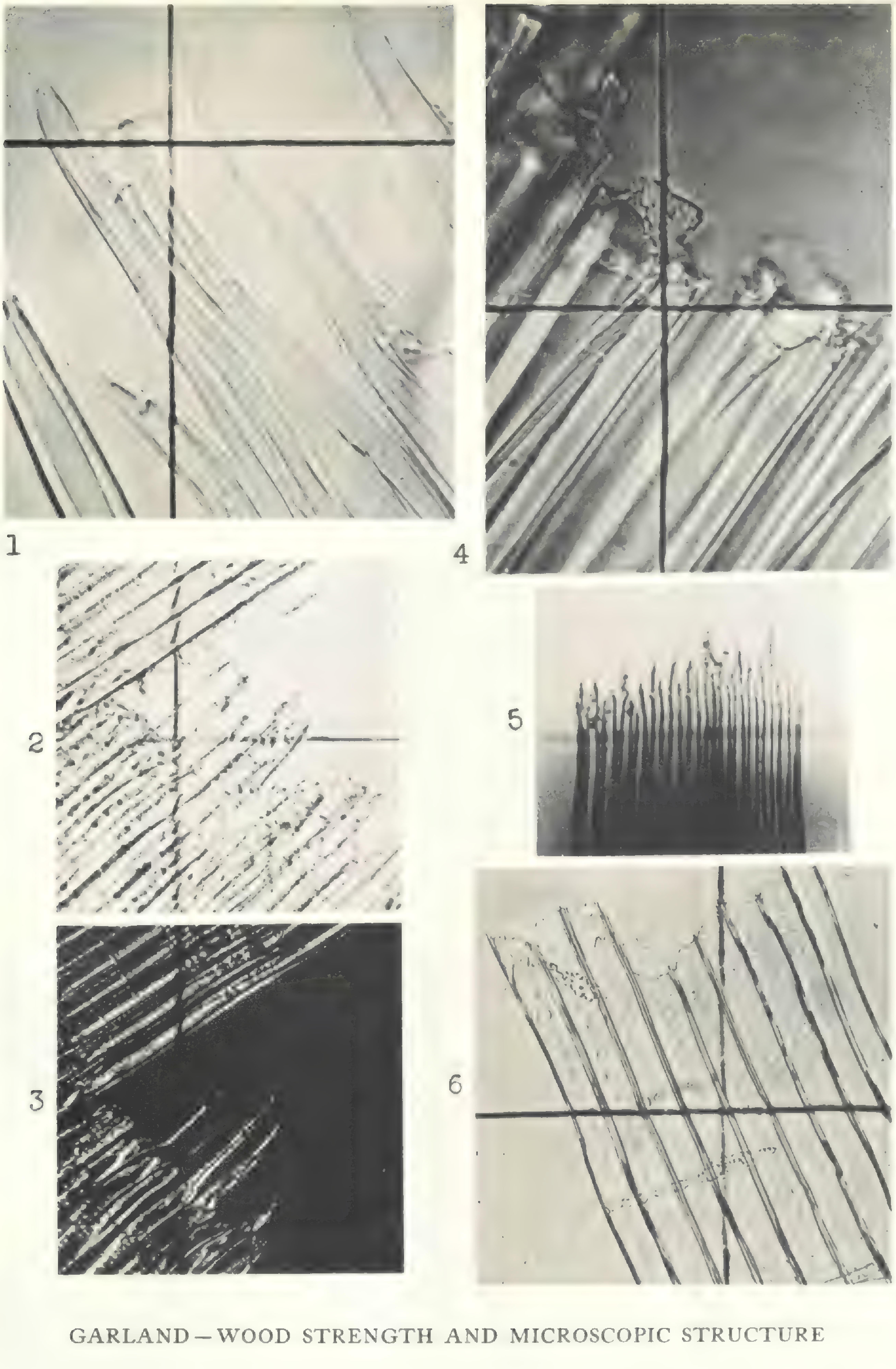
Fig. 2. Radial group of summerwood tracheids from green tension specimen 6-B-2, showing method of fracture common for strong fibers. The central layers of the secondary wall are unbroken and separation has occurred between the central and outer layers. Note sleeves and sheets of outer layer projecting. × 100.

Fig. 3. Same as fig. 2 with analyzer inserted. × 90.

Fig. 4. Radial group of summerwood tracheids from dry tension specimen 3-D-5, showing fracture of the ''pipe-organ'' type and separation along the fibrils. This specimen is of medium fibrillar angle (sine, .310) and is relatively strong. × 440.

Fig. 5. Radial group of summerwood tracheids from green tension specimen 9-A-4, showing typical spiral fracture of fibers of high fibrillar angle (sine, .510). × 100.

Fig. 6. Radial group of springwood tracheids from dry tension specimen 3-D-5, showing typical irregular fracture. × 100.



GARLAND—WOOD STRENGTH AND MICROSCOPIC STRUCTURE

Explanation of Plate

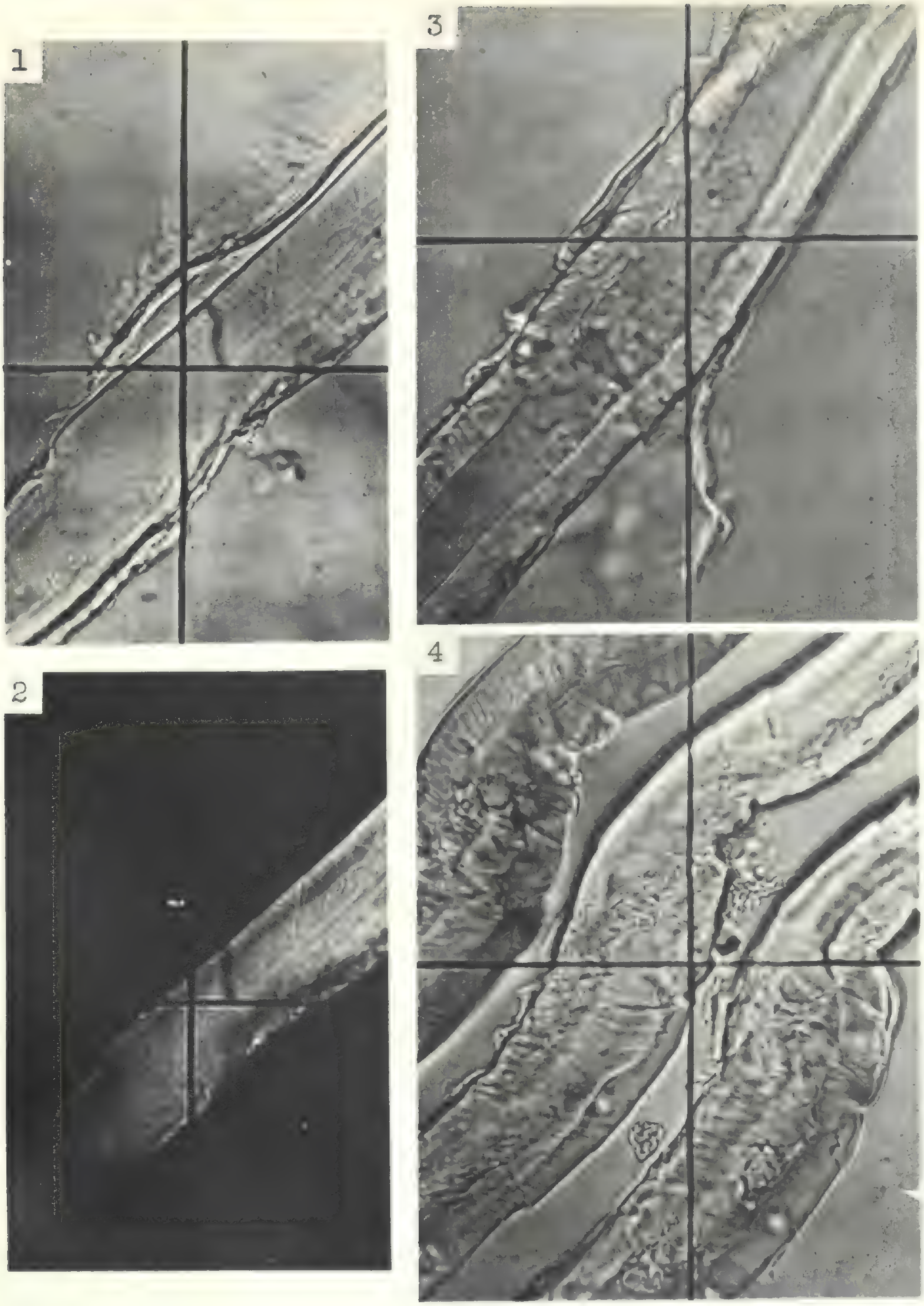
PLATE 5

Fig. 1. Summerwood tracheid from dry compression specimen 4-A-1 at fracture, showing prominent slip lines and rupture of the outer layer. The fragment of outer layer above belongs to an adjacent cell and has been partially separated at the middle lamella by maceration. × 440.

Fig. 2. Same as fig. 1 with analyzer inserted. × 396.

Fig. 3. Summerwood tracheid from green compression specimen 2-D-2 at fracture, showing slip line concentration typical of strong fibers and rupture between central and outer layers. × 440.

Fig. 4. Tangential view of a radial group of summerwood tracheids from dry compression specimen 2-B-2, showing prominent slip lines associated with displacements of wall material. The bend above is coincident with a ray crossing and the creases occur at the pits. × 440.



GARLAND—WOOD STRENGTH AND MICROSCOPIC STRUCTURE

Explanation of Plate

PLATE 6

Fig. 1. Summerwood tracheid from dry compression specimen 4-A-1 at fracture, showing prominent slip lines associated with displacements (diagonal shear) in the walls and with movement of the wall material into the lumen. × 440.

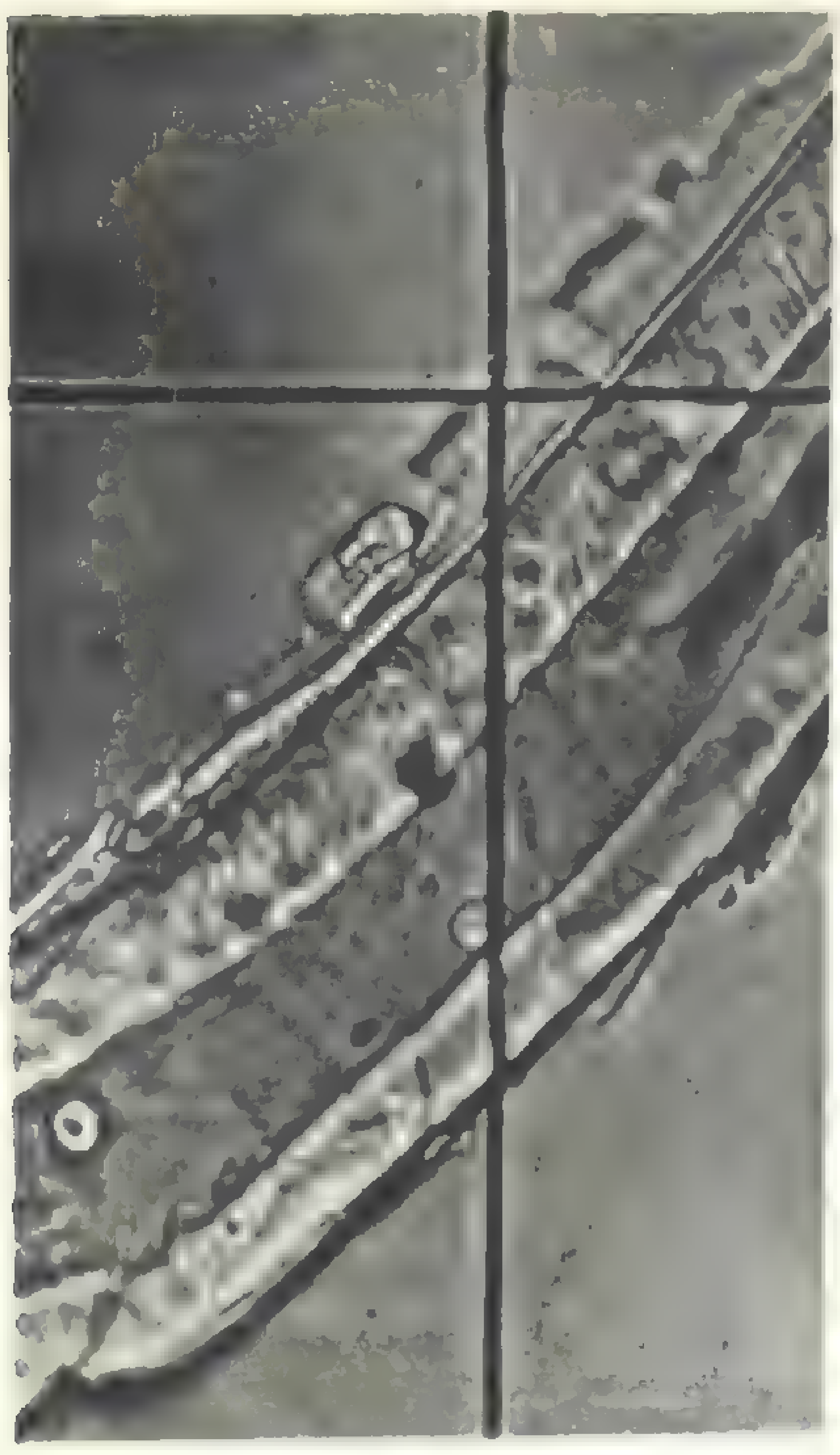
Fig. 2. Same as fig. 1 with focus on a sheet of outer layer at upper right showing it to be a remnant of an adjacent cell. × 440.

Fig. 3. Same as fig. 1 with analyzer inserted. × 396.

Fig. 4. Summerwood tracheid from dry compression specimen 7-B-4 at fracture, showing slip lines and separation of outer layer from central layer. × 440.

Fig. 5. Summerwood tracheid from green compression specimen 9-A-4 at fracture, showing few slip lines and thick outer layer which is apparently not closely associated with the central layer. This is a typical "compression wood" fiber with high fibrillar angle (sine, .490) and prominent checks in the central layer. × 440.

Fig. 6. Same as fig. 5 with analyzer inserted. × 396.



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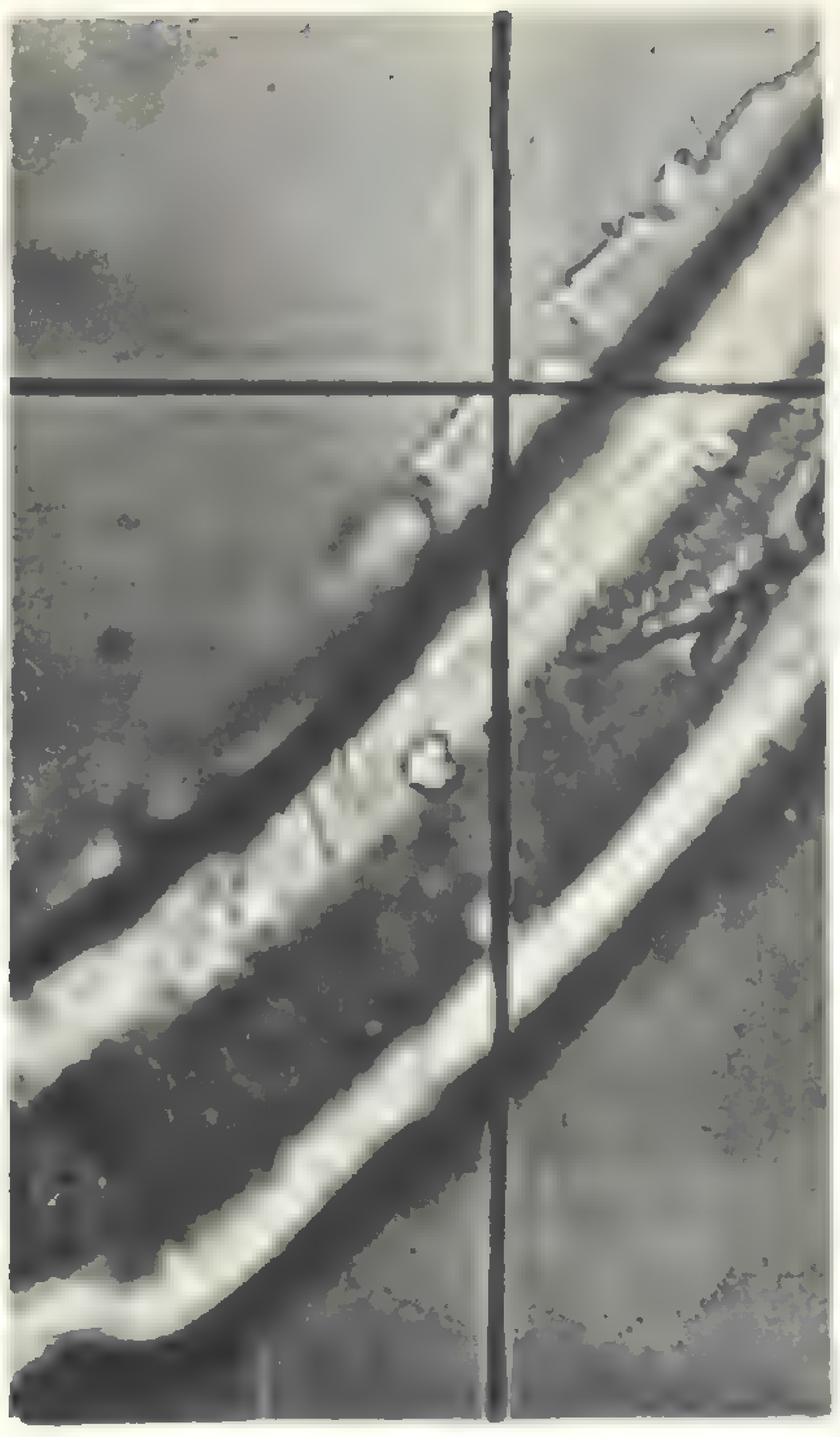

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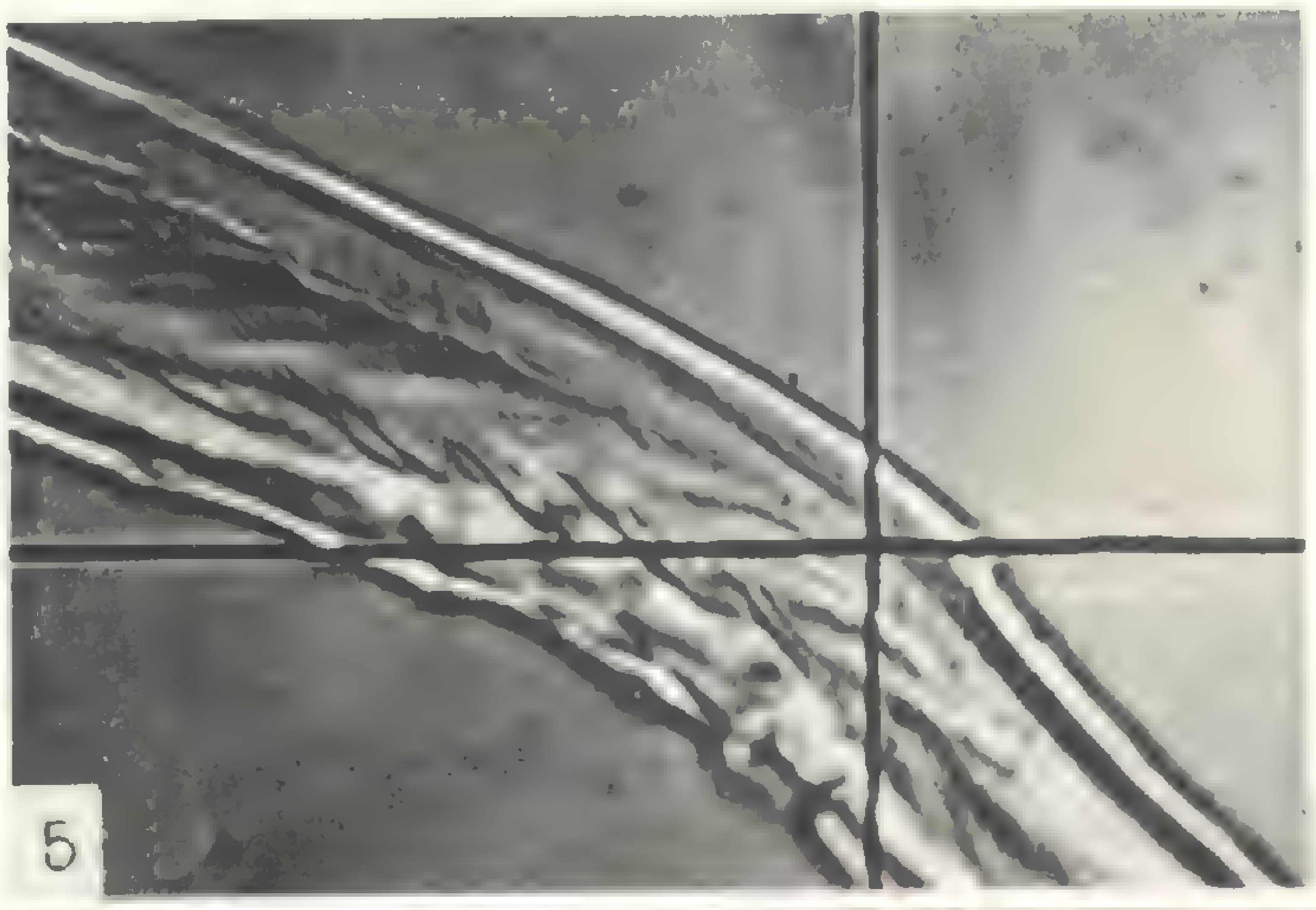

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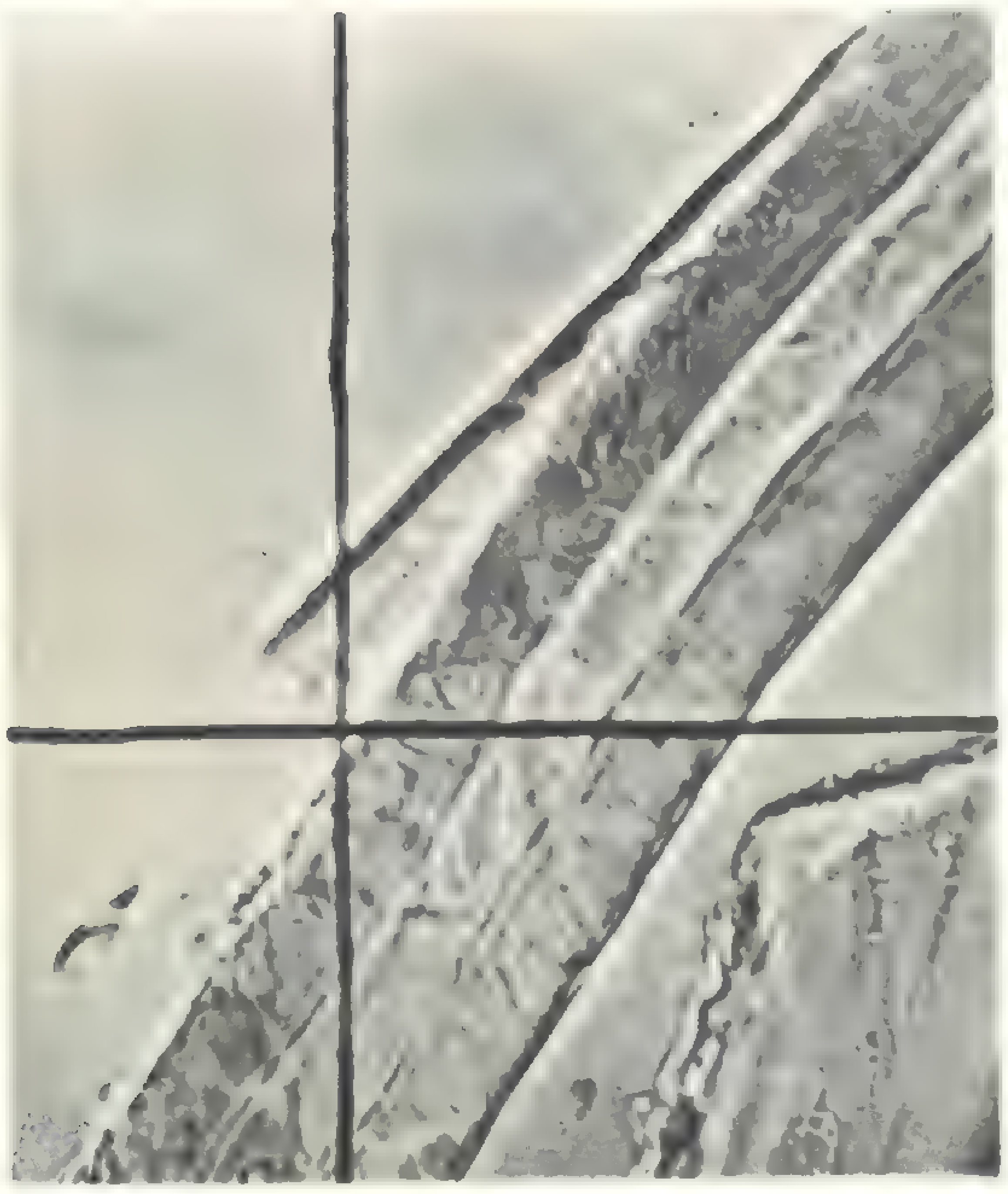

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GARLAND—WOOD STRENGTH AND MICROSCOPIC STRUCTURE

Explanation of Plate

PLATE 7

Fig. 1. Radial group of summerwood tracheids from green compression specimen 7-A-4 at fracture, showing method of separation that may occur between fibers of high fibril angle (sine, .450). Lateral rupture has occurred mostly within the central layer and has followed planes of slip lines and of fibril orientation. Focus on radial view at left. × 440.

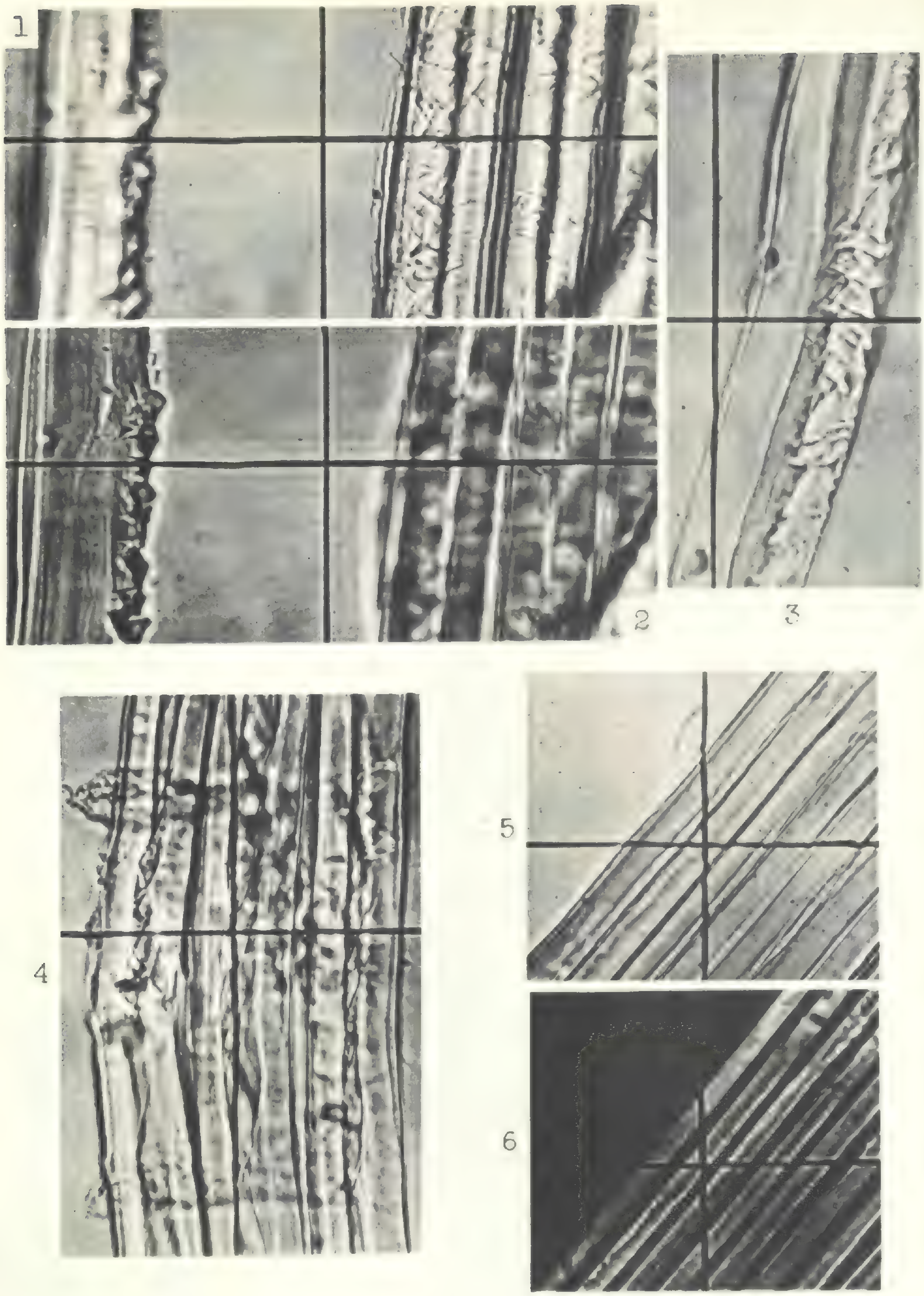
Fig. 2. Same as fig. 1 with focus on a single fiber that has become detached from the group and turned to present a tangential view. × 440.

Fig. 3. Summerwood tracheid from green compression specimen 7-A-4 at fracture, showing rupture of the central layer of the secondary wall due to lateral separation. × 440.

Fig. 4. Radial group of summerwood tracheids from dry compression specimen 9-D-4 at fracture, showing thick outer layer and scarcity of slip lines typical of fibers with high fibrillar angle (sine, .410). The fiber at the right has fractured along planes of the fibrillar checks. × 440.

Fig. 5. Group of summerwood tracheids from green tension specimen 7-A-4 of rather high fibrillar angle (sine, .390), showing thick outer layer and absence of checks. This specimen is relatively low in strength. × 440.

Fig. 6. Same as fig. 5 with analyzer inserted. × 396.



GARLAND—WOOD STRENGTH AND MICROSCOPIC STRUCTURE

Explanation of Plate

PLATE 8

Fig. 1. Summerwood tracheid from dry tension specimen 1-C-3 of medium fibrillar angle (sine, .330), showing relatively thick outer layer and prominent checks in the central layer. This specimen is weak in comparison with specimen 8-A-1 (figs. 3 and 4). × 440.

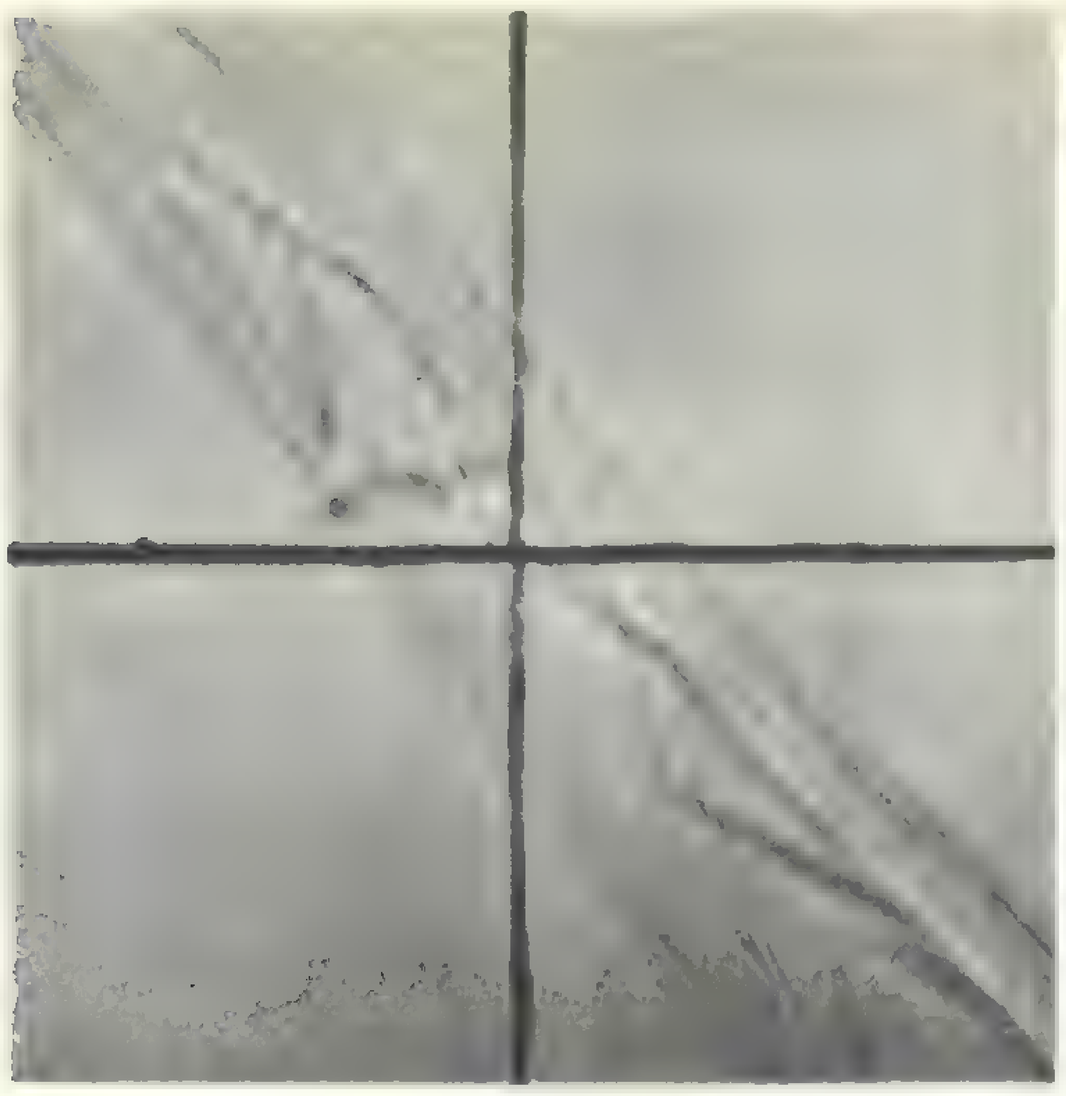
Fig. 2. Same as fig. 1 with analyzer inserted. × 396.

Fig. 3. Summerwood tracheid from dry tension specimen 8-A-1 of medium fibrillar angle (sine, .350) showing outer layer relatively thin and absence of checks. This specimen is strong in comparison with specimen 1-C-3. × 440.

Fig. 4. Same as fig. 3 with analyzer inserted. × 396.

Fig. 5. Summerwood tracheid from dry tension specimen 5-D-4 of low fibrillar angle (sine, .110) and relatively low strength showing slip lines which may have been present before the test. × 440.

Fig. 6. Same as fig. 5 with analyzer inserted. × 396.



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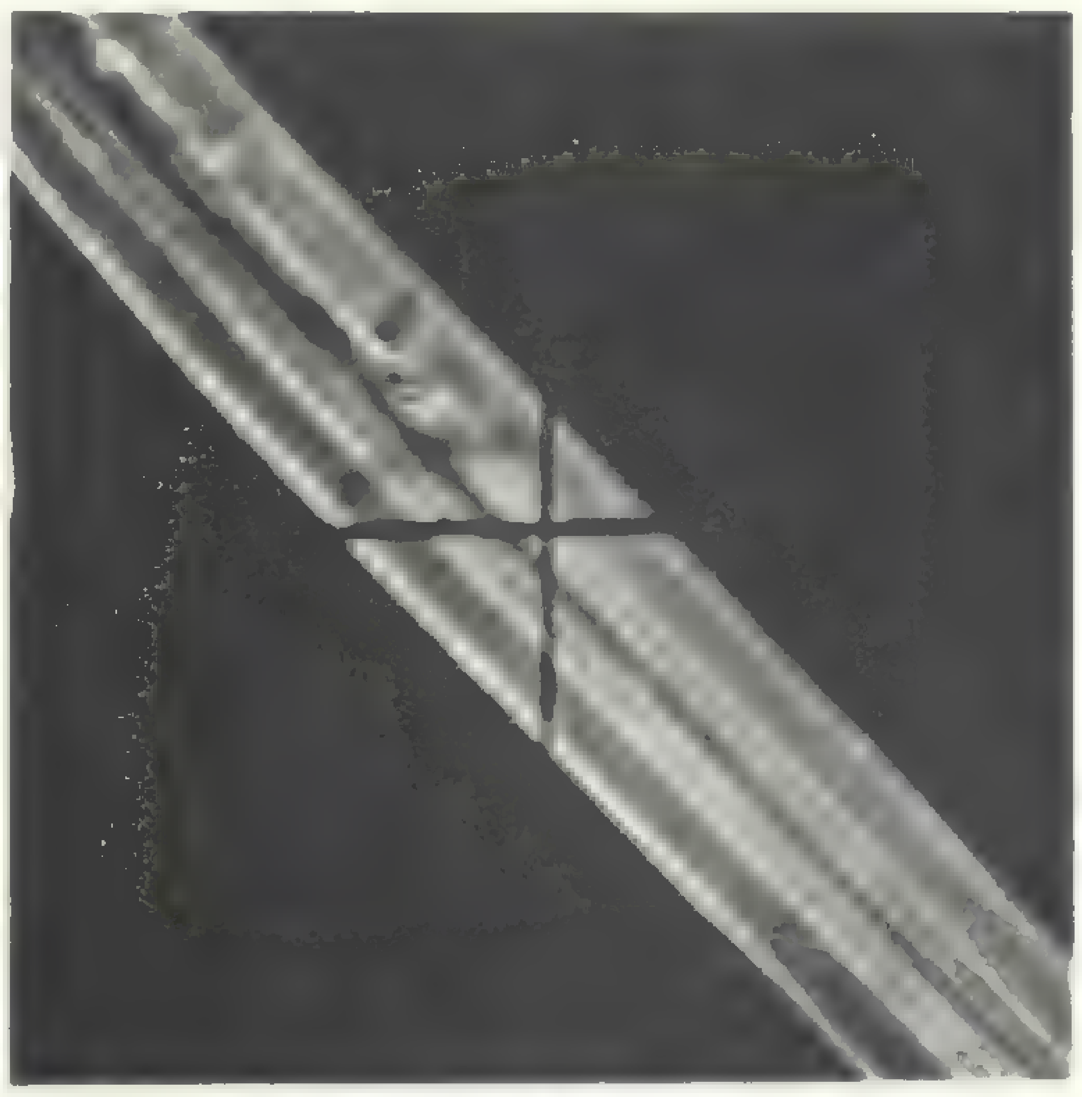

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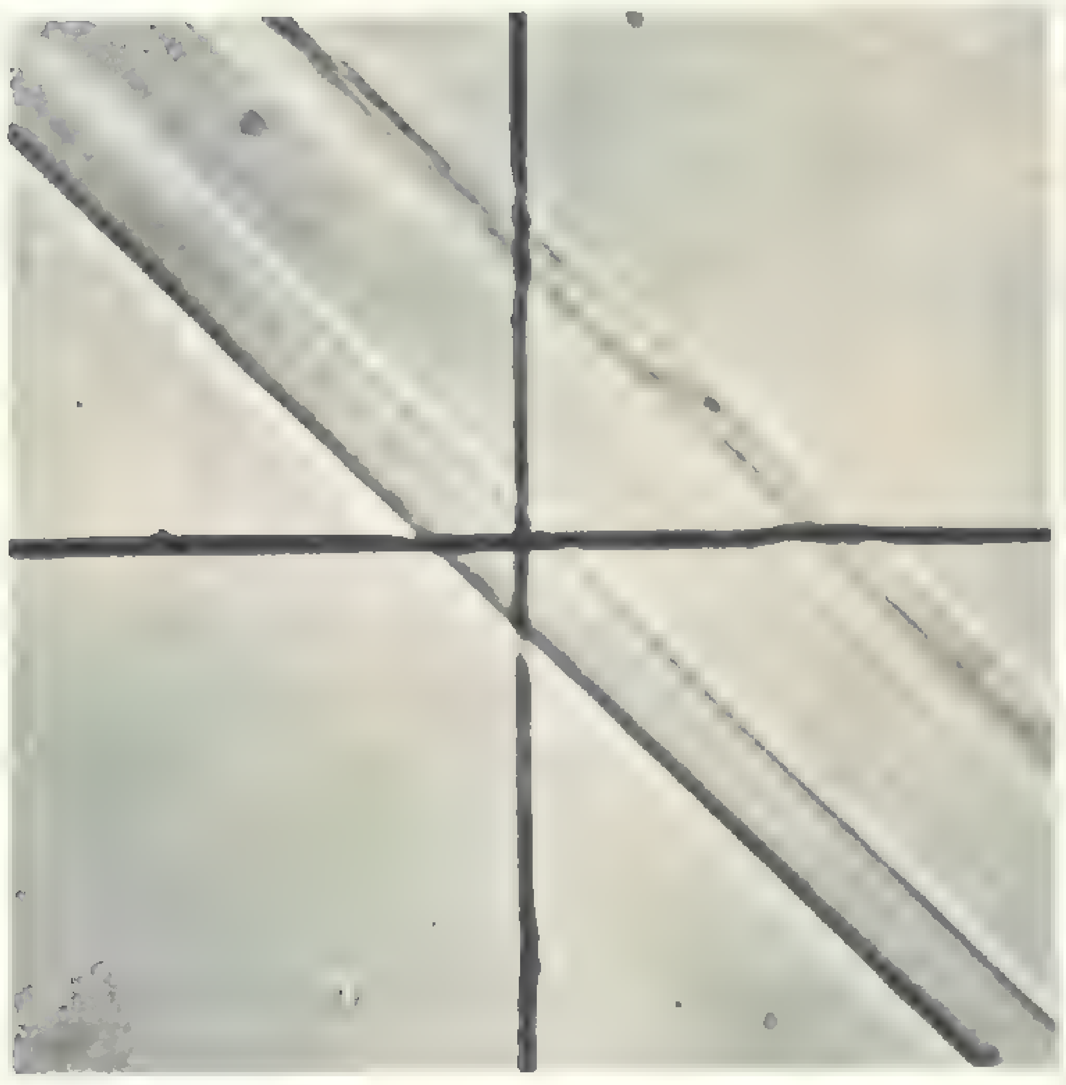

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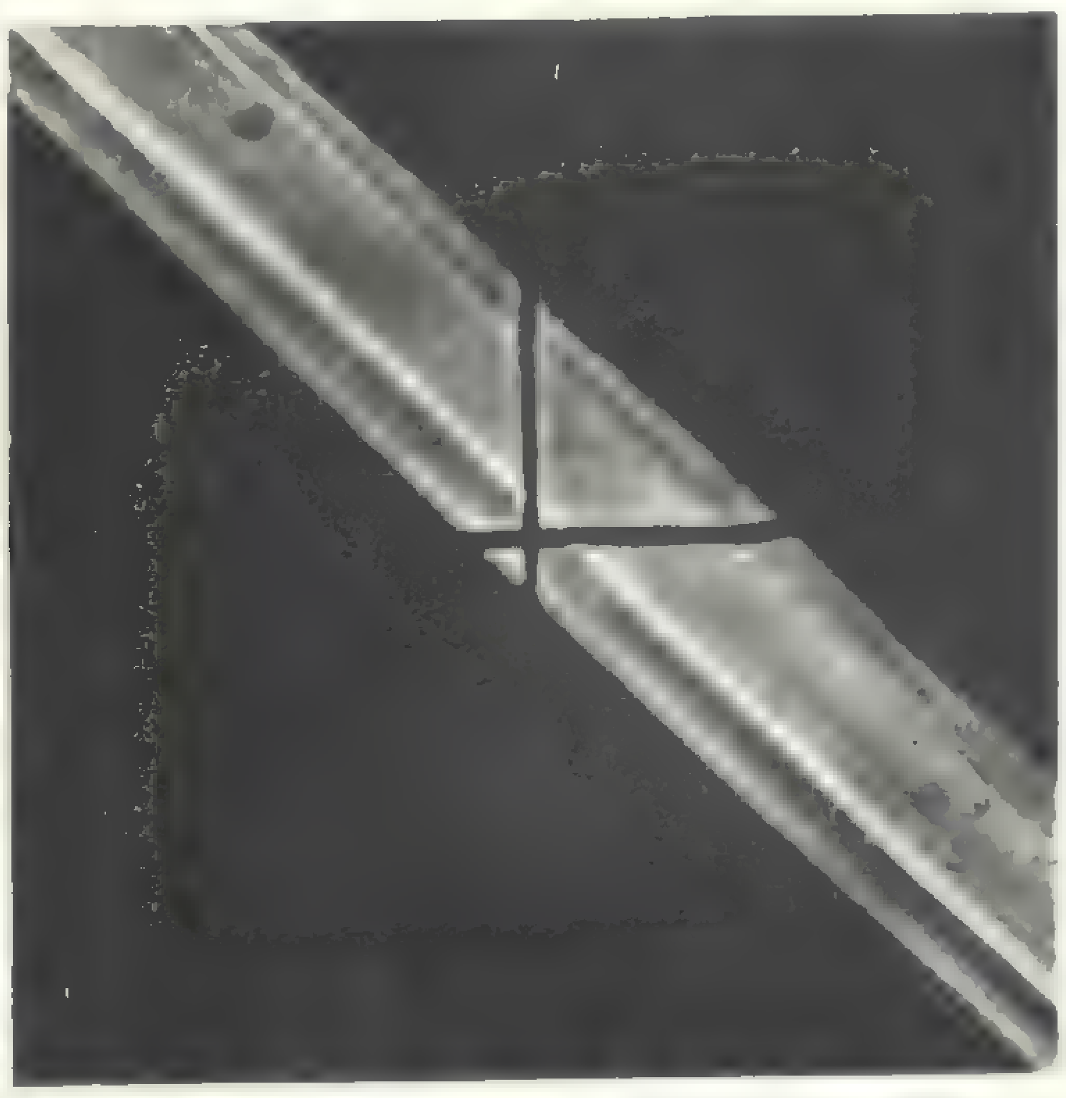

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GARLAND—WOOD STRENGTH AND MICROSCOPIC STRUCTURE

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NEW OR OTHERWISE NOTEWORTHY APOCYNACEAE OF TROPICAL AMERICA. VI[1]

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Mandevilla Lobbii Woodson, spec. nov., fruticosa volubilis; ramis sat gracilibus juventate dense minuteque puberulis tandem glabratis; foliis oppositis petiolatis ovato-ellipticis apice acute acuminatis basi rotundatis vel leviter cordatis 3.5–6.0 cm. longis 1.8–2.7 cm. latis firmiter membranaceis supra sparse pilosulis nervo medio basi pauciglanduligero subtus puberulis; petiolis 0.5–0.6 cm. longis puberulis; appendicibus stipulaceis minutissimis vix bene visis; racemis simplicibus lateralibus flores gilvos (?) 4–7 gerentibus; pedunculo petiolos ca. ter superante dense puberulo; pedicellis ca. 1 cm. longis minute puberulis; bracteis obovato-ellipticis acuminatis subfoliaceis 0.6–1.0 cm. longis minute puberulis persistentibus; calycis laciniis lanceolatis acuminatis 0.6–0.7 cm. longis extus sparse pilosulis squamellis multis attenuatis; corollae salverformis extus glabrae vel indistincte papillatae tubo 1.8 cm. longo basi et apice ca. 0.17 cm. diametro prope medium paulo inflato ibique staminigero, lobis late et oblique obovatis breviter acuminatis 1.5 cm. longis patulis; antheris 0.7 cm. longis basi truncatis vel paululo rotundatis glabris; ovario ovoideo glabro ca. 0.2 cm. longo; stigmate umbraculiforme 0.4 cm. longo longe apiculato; nec-

[1] Issued April 29, 1939.

tariis 5 emarginatis ovario multo brevioribus; folliculis ignotis.—PERU: data incomplete, *Lobb s.n.* (Herb. Naturhist. Mus., Wien, TYPE).

Closely allied to *M. Jamesonii* Woodson, but differing in the strikingly developed bracts which recall several species of the subgen. *Exothostemon.*

Mandevilla dissimilis Woodson, spec. nov., suffruticosa volubilis; ramulis teretibus juventate minute puberulis mox glabratis; foliis oppositis petiolatis oblongo-ellipticis apice acute acuminatis basi cordatis 4–5 cm. longis 1.8–2.5 cm. latis firmiter membranaceis supra minute puberulis tandem glabratis nervo medio basi pauciglanduligero subtus dense puberulis; petiolis 1.0–1.3 cm. longis minute puberulis; appendicibus stipulaceis minutissimis; inflorescentiis racemosis simplicibus folia subaequantibus flores gilvos (?) 8–10 gerentibus; pedunculo petiolos subaequante minutissime puberulo; pedicellis 0.4–0.5 cm. longis minutissime puberulis; bracteis attenuatis 0.3–0.4 cm. longis; calycis laciniis lanceolatis acuminatis 0.6–0.7 cm. longis minute puberulis; corollae infundibuliformis extus omnino minute puberulae tubo proprio 0.6 cm. longo basi ca. 0.15 cm. diametro, faucibus campanulatis 0.65 cm. longis, ostio ca. 0.45 cm. diametro, lobis late et oblique obovatis 0.6 cm. longis patulis; antheris inclusis 0.4 cm. longis basi truncatis; ovariis ovoideis minute puberulo-papillatis ca. 0.15 cm. longis; nectariis ovarium ca. dimidio aequantibus truncatis vel leviter emarginatis; stigmate umbraculiforme 0.3 cm. longo longe apiculato; folliculis non visis.—ECUADOR: "Andes Quitenses," data incomplete, *Spruce s.n.* (Herb. Naturhist. Mus., Wien, TYPE).

This species is closely allied to *M. equatorialis* Woodson, but appears to me sufficiently distinct for specific rank because of its considerably larger flowers with proportionally longer proper tube. The leaves, also, are broader, with a shorter petiole.

Fernaldia asperoglottis Woodson, spec. nov., suffruticosa volubilis; ramulis teretibus puberulis ad maturitatem glabrat-

is; foliis oppositis longiuscule petiolatis membranaceis late ovatis apice breviter subcaudato-acuminatis basi late sed haud profunde cordatis 3–12 cm. longis 2–7 cm. latis utrinque superne densius aspero-puberulis; petiolis 0.7–1.5 cm. longis puberulis; inflorescentiis pseudo-racemosis multifloris; pedunculo puberulo folia multo superante; pedicellis geminis ca. 0.4 cm. longis post maturitatem paulo accrescentibus; bracteis minute lanceolatis vix 0.2 cm. longis; calycis laciniis ovato-lanceolatis acuminatis ca. 0.2 cm. longis foliaceis extus pilosulis intus basi squama deltoidea erosa munitis; corollae pulchrae albidae extus minute pilosulae intus omnino dense arachnoideo-villosulae tubo proprio 0.3–0.4 cm. longo basi ca. 0.15 cm. diametro, faucibus late campanulato-conicis 1.5 cm. longis, ostio ca. 1 cm. diametro, lobis late ovatis obtusis 0.8–0.9 cm. longis patulis; antheris oblongo-sagittatis basi obtuse auriculatis 0.6 cm. longis glabris; ovariis oblongoideis ca. 0.15 cm. longis glabris; stigmate fusiformi apice obtusiusculo basi appendiculato-digitato ca. 0.2 cm. longo; nectariis 4 basi concrescentibus ovarium ca. dimidio aequantibus; folliculis (immaturis) falcatis leviter moniliformibus 18–20 cm. longis glabris. —MEXICO: GUERRERO: Temisco, Sierra Madre del Sur, north of Rio Balsas, Distrito Adama, trail east from Stamp Mill, cleared overgrown slope, alt. 315 m., frequent, scattered, Nov. 5, 1937, *Ynes Mexia 8751* (Herb. Missouri Bot. Garden, TYPE).

At first glance, this species recalls *Mandevilla convolvulacea* (A. DC.) Hemsl., because of the somewhat abbreviated corolla with broad, campanulate throat. However, it shows all the generic characters of *Fernaldia* very clearly. The small corolla, with exceptionally short throat, readily distinguishes *F. asperoglottis* from the other known species of the genus. The follicles are of especial interest, for they are the first records of fruit for *Fernaldia*. Those sent me, however, are too immature for examination of the seed.

Macrosiphonia Brachysiphon (Torr.) A. Gray var. **magnifica** Woodson, var. nov., a varietate typica corollis magnis (ca. duplo majoribus) differt, tubo proprio 2.5–2.7 cm. longo ca. 0.15 cm. diametro extus minute subarachnoideo-pilosulo, fau-

cibus subtubuloso-conicis 1.7–1.8 cm. longis, ostio ca. 0.6 cm. diametro, extus minute puberulo-papillatis, lobis oblique obovatis 2 cm. longis patulis.—Mexico: sonora: open granitic slopes, alt. 650–800 m., ridge south of Arroyo Gochico, east of San Bernardo, Aug. 5–9, 1935, *F. W. Pennell 19524* (U.S. Nat. Herb., type).

This variety bears flowers about twice the size of those of the typical variety of *M. Brachysiphon* (specimens of which I have seen from near San Bernardo). Since normal *M. Brachysiphon* is otherwise a remarkably constant species, confidence can be placed in the erection of *magnifica* in a varietal capacity, although I believe the characters insufficient to warrant specific rank.

STUDIES ON VARIATION IN GIBBERELLA SAUBINETII (MONT.) SACC. (FUSARIUM GRAMINEARUM SCHWABE)[1]

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Introduction

In recent years much attention has been given to variation in fungi, chiefly as a step in pathogenicity studies in combating diseases of economic plants. The exact nature of these variations has been, and still remains, very controversial. In artificial culture, variations may be in the form of sectors or islands in apparently homogenous cultures, or the whole culture may vary perceptibly from the parent organism. The variations may be only temporary, reverting to the parental type in the next cultural generation; they may persist through several generations and then revert to the parental type; or remain as permanent variants; or, they may in turn form still other variants.

Brierley ('31) summarizes the theoretical modes of origin of new forms as follows: "(1) by adaptation of an existing form, (2) by hybridization of two existing forms, or by some other mode of genetic fusion and segregation, and (3) mutation." He adds that what is apparently a new form may possibly be only the re-emergence and stabilization of a suppressed or latent character, or grouping of characters, or of a particular cyclogenic phase in a polyphasic organism.

The objects of the experiments described in the first part of the paper were: (1) to determine whether variation can be

[1] An investigation carried out at the Missouri Botanical Garden in the Graduate Laboratory of the Henry Shaw School of Botany of Washington University and submitted as a thesis in partial fulfillment of the requirements for the degree of doctor of philosophy in the Henry Shaw School of Botany of Washington University.

induced by altering environmental conditions, and to compare the variant with the parental type in order to obtain evidence of possible genetic change in constitution; (2) to determine whether there is a definite cycle of growth stages, such as mycelial, sporulating, and pionnotal, which can be influenced by environmental conditions; and (3) to observe whether the pionnotal stage reverts to the stage with aerial mycelium.

The experiments described in the latter part of this paper were devised to show whether, when contrasting monosporous strains are grown together on culture media, the hyphal anastomoses result in heterocaryosis, thus producing new strains.

Historical Review

Variations in fungi have been referred to as mutations, saltations, discontinuous variations, dissociations, and semi-permanent variations. De Vries ('06) used the term "mutation" for a means of change which lies in the sudden and spontaneous production of new forms from old stock. Muller ('22) refers to mutation as a variation in the individual gene. "Saltation" has been used more or less synonymously with mutation. However, it was probably used first by Stevens ('22) to designate heritable variations for which the sexual stages are not known, and in which the cytological conditions have not been thoroughly investigated. Das Gupta ('34) states that saltation includes only those variations which are of the order of mutation in higher plants. Brierley ('31) prefers to use the non-committal descriptive term "discontinuous variation," which "has no genetic implications." "Dissociation," as defined by Leonian ('32), the originator of this view, "is that phenomenon whereby a given organism traces the sphere of variability of the species." He states that no two members of a given species are identical, and that if tests could be sufficiently refined, differences between any two isolants of the same variety would probably be detected. Dissociations serve to bring forth such differences and to enlarge our species concept. Caldis and Coons ('26) state that the variants which they studied rep-

resent semi-permanent variations which differ from the parent form somatically rather than genetically. They suggest that the variations may be due to a nutritional disturbance which may be overcome when the necessary conditions are supplied.

Studies on variation in fungi under cultural conditions were recorded at least as early as 1908 by Edgerton, who considered one of his variant forms of *Glomerella* as a mutation. In a later publication ('14) he remarked that this mutation was no doubt the minus strain of this fungus. Crabill ('14) observed a mutation in a pure Petri-dish culture of *Phyllosticta,* and later ('15) he reported the sudden development of a minus strain from a plus strain in *Coniothyrium pirinum.* This phenomenon was observed four times in single spore cultures, and his explanation was that the minus strain was a "sport or mutant arising from the plus strain at irregular and unprognosticable intervals." Blakeslee ('20) observed two mutations in non-sexually propagated races of *Mucor genevensis.* Other recorded mutations are those of Burger ('21) in *Colletotrichum gloeosporioides;* Chodat ('26) in *Aspergillus ochraceus* and *Phoma alternariacearum;* Christensen ('26), Christensen and Davies ('37), in *Helminthosporium sativum;* Christensen and Stakman ('26), Stakman, Christensen, Eide, and Peturson ('29), and Stakman, Christensen, and Hanna ('29), in *Ustilago Zeae,* in which they reported numerous mutations in monosporous cultures; Newton and Johnson ('27) in *Puccinia graminis Tritici;* Sellsschop ('29) in *Gloeosporium;* Rodenhiser ('30) in *Phlyctaena linicola;* Blochwitz ('31) in *Citromyces luteus,* which was described at first as *Penicillium javanicum;* and Eide ('35) in *Gibberella Saubinetii,* in which he attributed the variations to true mutations or at least resulting from genotypic changes. Burkholder ('23) isolated the gamma strain of *Colletotrichum Lindemuthianum* from beans in a field where only the alpha and beta strains had been known. Since it was nearer to the beta strain in its range of susceptible hosts, he concluded that it was a mutation from that strain.

Following the studies of Stevens ('22) on *Helminthosporium,* Mitter ('29), in his work on saltations in the genus *Fu-*

sarium, found a greater difference between parent and variant than between species and species.

Horne and Das Gupta ('29) reported an "ever-saltating" strain in *Diaporthe perniciosa.* It was impossible to prevent saltation from occurring in every cultural generation. The resulting variant or strain was always the same. The ability of the strain to saltate was independent of the medium and was inherent in the strain itself. In 1934, Das Gupta, after further work on these strains, reported saltation to be a conversion phenomenon. He concluded that properties of both strains were included in a single culture of DH_C and even in a single hypha but that the properties might be spatially separated in the hypha. One strain of DH_F had no visible expression in the presence of the other strain DH_C. However, if small segments were cut from a young hypha of DH_C mycelium, the majority would develop into DH_F, and the remainder into DH_C. Also the young DH_C mycelium was able to convert a DH_F culture into DH_C.

Matsuura ('30, '30A, '32) described four types of saltations in *Ophiobolus, Brachysporium, Alternaria,* and an Ascomycete from pears. Some of these saltations partially or totally reverted.

Leonian ('26) reported a reversible mutation in *Phytophthora.* Strain I gave rise at times to strain IV or a mixture of I and IV, and strain IV by mutation resulted at times in strain I.

Chaudhuri ('24) described some saltations which were permanent on Coons' agar and on oatmeal agar, but which reverted to the original when transferred to potato-mush agar. Transfers made to Coons' or oatmeal agar from the potato-mush agar did not produce the variant again.

The preponderance of cases of saltations or mutations have been of a varietal or specific nature. However, Wiltshire ('29, '32) reported a reversible saltation, where a *Stemphylium* culture in the presence of a bacterial colony gave rise to an *Alternaria* colony which in turn produced the *Stemphylium* colony again. Brett ('31) found a cyclic saltation in *Stemphylium.*

Within a colony of *Stemphylium,* dark spore heads were produced. Spores from these gave rise to *Alternaria* colonies in which the spores were produced in chains. The *Alternaria* spores gave rise to *Stemphylium* again, completing the cycle. Das Gupta ('30) working with *Cytosporina,* obtained not only the characteristic bent filiform spores, but also oval spores, characteristic of the genus *Phomopsis.* Christensen ('32) observed that sectors formed in monospore cultures of *Pestalozzia funerea* produced colonies conforming to those described for *Monochaetia.* Cultures of the *Monochaetia* type were also obtained from spores produced in pustules of *Pestalozzia funerea* on long-leaf pine. Saccardo (1884) distinguished the genus *Pestalozzia* from the genus *Monochaetia* on the number of setae, the former having two to six and the latter only one. Christensen believed that our previous conception of the genus *Pestalozzia* should be modified to include this form with one seta.

Orthogenetic or unidirectional saltations have been reported by Crabill ('15) in *Coniothyrium,* referred to above; and Das Gupta ('30) in *Cytosporina.* A particular strain may be reached in one saltation, or two or three saltations may take place before it has been developed. For example, Brown ('26) and Mohandra ('28) found that sometimes strain I gave rise to strain III, and at other times it produced strain II. The latter did not remain stable but gave rise to strain III. Das Gupta ('30) observed a particular strain in *Cytosporina* to be reached by one, or by a series of three saltations.

Burkholder ('25), working with *Fusarium mortiiphaseoli* grown in culture for a period of five years, discovered that it varied both in morphological characters and in virulence but would revert when inoculated into a bean plant and re-isolated. He thought that this might explain the great number of species and varieties in *Fusarium.* Chaudhuri ('31) has found the same to be true with some fungi with which he worked. Palmiter ('34) suggested, from his observations of cultures of *Venturia inaequalis,* that this species was not homogeneous but composed of many strains differing physiologically and morphologically.

La Rue ('22), from his work on *Pestalozzia Guepini,* stated that he found no evidence that distinct lines could be established by selection. However, Curzi ('30) reported that by selecting transfers of sectors of a monoconidial culture of *Fusarium Moronei,* he obtained two non-reversible strains. Strain alpha was the result of selection, through several generations, of the sector having the most profuse aerial mycelium; likewise, strain gamma was secured by selecting the sector having the scantiest aerial mycelium.

Greene ('33) found two types of variants in *Aspergillus Fischeri.* In the first type, the ascospores produced cultures practically identical with the original stock culture, while the conidia continued to give rise to the variant form. In the second type both ascospores and conidia produced the variant form.

Experimental Work

A. Sources of Cultures.—Cultures of two strains of *Gibberella Saubinetti* (Mont.) Sacc. were obtained in the summer of 1937 from Dr. Carl J. Eide, of the Division of Plant Pathology and Botany at the University of Minnesota. He collected the original perithecial material on old corn stubble in grain fields in Minnesota in 1932-1933.[1] These strains were designated by him as A36–1–V and A43–4–I–I. The first was obtained from a single ascospore of the original perithecial material but did not in turn produce perithecia in culture. The second culture was from an ascospore of a perithecium which formed on an old piece of inoculum after it had been transferred to fresh agar in a flask. It had been noted that the original ascospore culture, that from the ascus of a perithecium on corn stubble, had not formed fertile asci in culture on synthetic media. The same is true of this variant or strain.

B. Materials and Methods.—For the greater part of the culture work the substratum used was potato-dextrose agar. The special media used were Brown's "synthetic potato-dextrose" agar, Coons' synthetic medium, Leonian's agar, and

[1] These strains, along with some others, were used in investigations for his doctoral thesis (Eide, '35).

Richards' agar. Malt extract agar medium was used for some of the stock cultures.[2]

Single conidia were isolated with the Zeiss, and Bausch and Lomb micro-manipulators, using a glass needle in the manner described by Dickinson ('33). The conidia were immediately transferred to fresh drops of agar on cover slips which were then inverted on Van Tieghem cells in Petri dishes lined with moist filter-paper. After germination of the conidia, the agar drops were transferred to culture media in Erlenmeyer flasks, Petri dishes, or test-tubes. Where cultures produced no conidia, hyphal tips were cut off and used. This was done by transferring a bit of the mycelium to "water agar"[3] in Petri dishes. The scanty growth on this substratum made possible the isolation of single hyphae. In one instance the cutting tool consisted of a small piece of safety razor blade soldered to the end of a sewing needle, as described by Eide ('35). At another time, fine dissecting scissors were used. The tips of the hyphae were cut off under a dissecting microscope and, with a small portion of the agar, were transferred by means of a sterile instrument to fresh agar drops on cover slips. After the mycelia had developed slightly, the drops were transferred to media in test-tubes, Petri dishes, or Erlenmeyer flasks, as in the case of the conidia.

For cytological study, perithecia were dissected from the agar culture, killed and fixed in Hermann's fluid, embedded in paraffin, and serial sections cut at 7 microns. The stain used was Haidenhain's iron-alum haematoxylin, with phloxine as a counter-stain. The results were fairly good.

[2] The *potato-dextrose* agar consisted of: peeled potatoes, 400 gms.; dextrose, 10 gms.; agar, 17 gms.; and distilled water, 1 liter. *Brown's "synthetic potato-dextrose" agar:* glucose, 2 gms.; asparagin, 2 gms.; K_3PO_4, 1.25 gms.; $MgSO_4$, 0.75 gms.; agar, 17 gms.; and distilled water, 1 liter. *Coons' synthetic medium:* sucrose, 7.20 gms.; dextrose, 3.60 gms.; $MgSO_4$, 1.23 gms.; KH_2PO_4, 2.72 gms.; KNO_3, 2.02 gms.; agar, 17 gms.; and distilled water, 1 liter. *Leonian's agar:* peptone, 5 gms.; KH_2PO_4, 1 gm.; $MgSO_4$, 1 gm.; dextrose, 20 gms.; agar, 17 gms.; and distilled water, 1 liter. *Richards' agar:* cane sugar, 50 gms.; KNO_3, 10 gms.; KH_2PO_4, 5 gms.; $MgSO_4$, 2.5 gms.; $FeSO_4$, a trace; agar, 17 gms.; and distilled water, 1 liter. *Malt extract agar:* malt extract, 33.5 gms.; agar, 20 gms.; and distilled water, 1 liter.

[3] "Water agar" consisted of: agar, 1.5 gms.; and distilled water, 100 cc.

Small blocks of the mycelial culture of variants on agar were killed and fixed in Hermann's fluid, and embedded in celloidin. Serial sections were cut at 7½ microns (Foster, '26) and stained in Haidenhain's iron-alum haematoxylin and phloxine. The nuclei and cell walls were well differentiated, but individual hyphae could not be easily traced because of the compacted condition of the mycelium.

For the study of hyphal anastomoses, the following procedure was used: Conidia from two contrasting strains were allowed to germinate on a thin agar drop on a cover slip suspended over a Van Tieghem cell on a glass slide. Anastomoses of the hyphae were observed under the high power of the microscope, and camera-lucida drawings were made. For the stained preparations of hyphal anastomoses, the same procedure was used except that the agar drop was placed on the slide instead of the cover slip. The same killing fluid and stains were used as for perithecia. Differentiation of the septa was difficult because the greater part of the stain was removed from them in order to destain the agar drop.

C. Types of Strains at the Beginning of the Experiments.—A43–4–I–I, when grown on potato-dextrose agar in Petri plates, produced only a scant amount of white to pale pink aerial mycelium. The 2¼–2½-cm. salmon buff center of the upper surface was sometimes surrounded by two narrow bands, a wide band, and a narrow border. The first of these was purplish gray, the second vinaceous purple, the third purplish gray, and the border of submerged hyphae was vinaceous purple.[4] In other cases, the two narrow bands were absent (pl. 9, fig. 1). The center of the reverse was the same pattern as the upper surface, with the following colors, beginning at the center: apricot buff, dull violet black, dark vinaceous purple, dull violet black, and the border of dark vinaceous purple. There were numerous rudimentary perithecia on the upper surface. The dark vinaceous purple color was due to very numer-

[4] Colors given are those of Ridgway's "Color Standards and Color Nomenclature." 1912.

ous short thick-walled dark blue cells embedded in the agar. Conidia were abundant.

A36–1–V, when grown on potato-dextrose agar in flasks or Petri plates, produced an abundance of pale pink with some clay-colored aerial mycelium, cottony at first, then compacted with age (pl. 9, fig. 2). The bottom of the culture was dahlia purple to blackish red. The upper surface was level. Empty perithecia were numerous over the entire surface of the agar and many were embedded in it. Conidia were moderately numerous.

For convenience in this paper, the former strain will be referred to as A, and the latter as B.

D. Preliminary Cultural Work.—In order to determine the relative stability or variability in each strain, a number of conidia were isolated and grown under ordinary laboratory conditions on potato-dextrose agar. Forty-six conidia were isolated from strain B and transferred to agar drops in the manner described under "Materials and Methods." After germination of the conidia, the agar drops were transferred to potato-dextrose agar slants in test-tubes where they were allowed to grow until the surface of the medium was covered. No variation appeared in the test-tube cultures. Transfers were made in triplicate from each of the 46 test-tubes to potato-dextrose agar in Petri plates. After 25 days, the cultures appeared uniformly constant. About as much variation appeared between the plates from one conidium as between the sets of triplicates. Two and one-half months later, transfers were again made in triplicate to potato-dextrose agar in Erlenmeyer flasks. This time two types of variations appeared in six of the sets of triplicates, in from one to three flasks of each set (table I). The remaining 126 flasks were of the "normal"[5] type for B.

Transfers of these variant cultures were made to Leonian's agar in Erlenmeyer flasks, along with transfers of the pa-

[5] "Normal" as used in this paper refers to the original B or original A when grown on potato-dextrose agar.

TABLE I

VARIATION IN SIX SETS OF TRIPLICATES OF SERIES B GROWN ON POTATO-DEXTROSE AGAR IN FLASKS AT ROOM TEMPERATURE

Triplicates	Form of variant	Color		Amount of aerial mycelium	Rudiments of perithecia
		Upper surface	Reverse		
B 5 3 flasks B35 2 flasks B44 2 flasks	Islands	"Normal" except for white islands	Normal	Much. Islands extended slightly above remainder of colony	Very few
B26 2 flasks B32 1 flask B45 2 flasks	Whole colony	Hay's maroon to acajou red	Normal	Little	Very numerous on surface and embedded in agar

rental type. B 26, B 32, and B 45[6] produced cultures identical with the parental type, while transfers from the white islands of B 5, B 35, and B 44 all produced cultures which were about 4 cm. tall and very cottony, in contrast to the parental type which was about 1 cm. tall, with the aerial hyphae more yellowish brown. Perithecia were not so abundant in the variant type and were embedded in the agar.

Cultures B 5–1, B 35–1, and B 44–1, from Leonian's agar, were grown again on potato-dextrose agar in flasks at the same time as B 5 of the parental type. The resulting cultures showed that B 35–1 and B 44–1 had reverted to the original "normal" B type identical with B 5, while B 5–1 remained a white cottony variant.

[6] The system of nomenclature used in this series of cultural experiments is as follows: A or B represents the original cultures with which this work was begun. The arabic numeral following is the number of the conidium isolated at random from that culture. Another arabic numeral following a dash represents the variant (island or sector) from this type. For example, A17–1 represents the culture from the first sector or island from the seventeenth conidial isolate of series A. If two sectors are formed in the same culture of A17, they are then designated as A17–1 and A17–2. If A17–1 again forms a sector, it will be designated as A17–1–1. This system was suggested by Dr. E. C. Stakman as a graphic way of recording the genealogy of each variant.

B 5 and B 5–1 were included in the experiment on "Attempts to Induce Variation in Strains," to be described later in this paper. Up to the present time B 5–1 has remained stable.

Of 46 single conidial cultures, 40 have remained stable through five cultural generations on potato-dextrose agar extending over a period of ten months; 6 formed variants in the fourth cultural generation. Three variants produced the parental type when transferred to Leonian's medium. Two of the remaining three reverted to the parental type when transferred from Leonian's medium to potato-dextrose agar again. One variant has remained stable through five cultural generations and on various media.

Fifty-two single conidial isolates were made from culture A in the same manner as described for culture B. No variations appeared in the test-tubes, but when transfers were made in

TABLE II

VARIATION IN FOUR SETS OF TRIPLICATES OF SERIES A GROWN ON POTATO-DEXTROSE AGAR IN PETRI PLATES AT ROOM TEMPERATURE

Triplicates	Form of variant	Color		Amount of aerial mycelium	Rudiments of perithecia
		Upper surface	Reverse		
A4 1 plate	Whole culture	Salmon orange with Eugenia red bands	Cinnamon rufous with Eugenia red bands	Some in center, border submerged	None
A17 1 plate	Sector	Same as above	Same as above	Same as above	None
A24 1 plate	Two sectors	Same as A17 with addition of dark purple zone toward center	Same as upper surface	Same as above	None
A43 1 plate	Whole culture	Salmon orange center, wide zone of dark greenish black, and a narrow zone of Eugenia red	Same as upper surface	Only scant amount on the dark zone	None

TABLE III

VARIATION IN FOURTEEN SETS OF TRIPLICATES OF SERIES A GROWN ON POTATO-DEXTROSE AGAR IN FLASKS AT ROOM TEMPERATURE

Triplicates	Form of variant	Color		Amount of aerial mycelium	Rudiments of perithecia
		Upper surface	Reverse		
A 5 1 flask A 7 2 flasks A 9 1 flask A15 1 flask A25 2 flasks A37 1 flask A45 1 flask	Whole culture	Light salmon orange center, wide dark purple band, and light salmon border	Same as upper surface	Very slight growth	Abundant on surface
A 8 2 flasks A12 1 flask A20 1 flask A21 3 flasks A23 2 flasks A46 1 flask	Whole culture	Same as A5 but with Eugenia red border	Same as A5 but with Eugenia red border	Very slight growth	Abundant on surface
A35 1 flask	Three sectors	Light salmon orange with 4 concentric narrow bands of light Eugenia red	Same as upper surface	None	None

triplicate to potato-dextrose agar in Petri plates, variations appeared in the four sets of triplicates which are recorded in table II. All except A17–1 produced the parental type in the next cultural generation, on potato-dextrose agar. About three months later, transfers were again made in triplicate to potato-dextrose agar in Erlenmeyer flasks, and the 14 variants which appeared this time were recorded in table III. All these possible variations, A5, A7, A8, A9, A12, A15, A20, A21, A23, A25, A35 (three sectors), A37, A45, and A46 were replated on potato-dextrose agar, and, with the exception of A35–1 (sector 1 of A35), all the plates showed the characters of the parental type.

E. Attempts to Induce Variation in Strains.—Since strains A and B were found to be fairly stable in the preliminary experiments when grown on potato-dextrose agar at room temperature, the cultures were grown on different substrata and

TABLE IV

VARIATION IN MACROSCOPIC CHARACTERS OF A17 GROWN ON VARIOUS MEDIA AT DIFFERENT TEMPERATURES

A 17	Richards' pH 4.5	Leonian's pH 4.8	Potato-dextrose pH 5.8	Coons' pH 6.5
		18° C.		
Color upper surface	Flesh-color mottled with Indian lake, dark purple border	Dark purple with wide rose-pink border	Seashell pink center, carmine border, remainder dark purple with slight mottling of seashell pink	Salmon buff center, remainder dark purple with slight mixture of salmon buff
Color reverse	Salmon with dahlia-purple mottling and dark purple fringed border	Dark purple with Vandyke red border	Same as upper but apricot buff instead of seashell pink	Same as upper
Type of growth	Uniform medium-heavy growth of aerial hypae	Uniform medium-heavy growth of aerial hyphae	Center and spots of medium-heavy growth of aerial hyphae, remainder light growth	Uniform light growth of aerial hyphae
Topography	Deeply wrinkled	Concentric furrow, few short radial furrows, lobed margin	Very shallow concentric furrow, and large shallow wrinkles	Short radial furrows, very uneven margin
Rudiments of perithecia	Few, small	Very numerous	Very numerous	Very few

at different temperatures in order to learn whether variations could be induced. Consequently, A17, A17–1, A4, A24, A43, A35, A35–1, B5, and B5–1 were grown in duplicate on Brown's "synthetic potato-dextrose" agar, Coons' synthetic medium, Leonian's agar, potato-dextrose agar, and Richards' agar at 18°, 20°, 25°, and 30°C. and the macroscopic characters recorded after 25 to 30 days. With the exception of A17–1, which produced no conidia and in which hyphal tips were substituted, single conidial isolates were used.

On Brown's medium (pH 5.6), A17 showed the appressed type of growth, or with very little aerial hyphae in the center. The color of both upper and reverse surfaces was seashell pink at temperatures 18°, 20°, and 25° C. At 30° C. the color was

TABLE IV (Continued)

A 17	Richards' pH 4.5	Leonian's pH 4.8	Potato-dextrose pH 5.8	Coons' pH 6.5
		20° C.		
Color upper surface	Salmon with very light mottling of Indian lake with fringe of dark purple	Center and wide border rose pink, wide uneven band of dark purple around center	Seashell pink center, carmine border, remainder dark purple with very slight mottling of seashell pink	Salmon buff center, remainder dark purple
Color reverse	Same as upper	Same as upper	Same as upper but carmine instead of rose pink	Same as upper but apricot buff instead of seashell pink
Type of growth	Uniform light growth of aerial hyphae	Uniform medium-heavy growth of aerial hyphae	Uniform light growth of aerial hyphae except center of very light aerial growth	Uniform light growth of aerial hyphae
Topography	Entire surface deeply wrinkled	Very shallow concentric furrow, slight radial furrowing, very uneven margin	Very shallow concentric furrow, hint of radial furrows around center	Level, no furrows
Rudiments of perithecia	Numerous	Numerous	Very numerous	Very few

pale salmon. The surface was smooth and no rudiments of perithecia were formed. Variations on other media are shown in table IV.

Growth of A17–1 on Brown's medium was appressed at 18° C., and appressed with few aerial hyphae at all other temperatures. The color was seashell pink; the surface was level, with no wrinkles or furrows; and no rudiments of perithecia were formed. Variations on other media are shown in table V.

A4, on Brown's medium, was mostly of the appressed type with very few aerial hyphae in the center. At 20° C., the growth did not exceed 1 cm. in diameter and developed no color. At 18° and 25° C., it was seashell pink, and at 30°, pale salmon color with orange pink reverse. The surface was

TABLE IV (Continued)

A 17	Richards' pH 4.5	Leonian's pH 4.8	Potato-dextrose pH 5.8	Coons' pH 6.5
		25° C.		
Color upper surface	Salmon	Center and border flesh pink, remainder dark purple mottled with flesh pink	Orange pink with radiate splashes of dark purple	Salmon buff with wide border of dark purple
Color reverse	Salmon	Same as upper but carmine instead of flesh pink	Cinnamon rufous with radiate splashes of dark purple	Same as upper but salmon instead of salmon buff
Type of growth	Mostly appressed, only very slight uniform growth of aerial hyphae	Felt-like growth of aerial hyphae	Uniform medium-heavy growth of aerial hyphae	Uniform light growth of aerial hyphae
Topography	Entire surface deeply wrinkled	Very shallow concentric furrow	Very shallow concentric furrow, hint of radial furrows or large wrinkles	Level except for very shallow concentric furrows near center
Rudiments of perithecia	None	Numerous	None	None
		30° C.		
Color upper surface	Light apricot orange	Chatenay pink	Apricot buff	Light salmon orange
Color reverse	Apricot buff	Apricot buff, very deeply mottled with carmine	Apricot buff	Light salmon orange
Type of growth	Appressed mostly; very slight growth of aerial hyphae	Uniform medium-heavy growth of aerial hyphae	Appressed except light growth of aerial hyphae in center and furrows	Appressed
Topography	Entire surface deeply wrinkled	Deep concentric furrow or none near center; 18–20 radial furrows	Level except 18–20 shallow radial furrows	Level except few shallow wrinkles in center
Rudiments of perithecia	None	None	None	None

TABLE V

VARIATION IN MACROSCOPIC CHARACTERS OF A17-1 GROWN ON VARIOUS MEDIA AT DIFFERENT TEMPERATURES

A 17-1	Richards' pH 4.5	Leonian's pH 4.8	Potato-dextrose pH 5.8	Coons' pH 6.5
		18° C.		
Color upper surface	Flesh pink	Alizarine pink; sector 1—rose red; sector 2—alizarine pink with rose red border	Orange pink with slight mottling of dark purple	Orange pink with light fringe of dark purple
Color reverse	Deep seashell pink	Acajou red with apricot buff margin; sector 1—Vandyke red; sector 2—acajou red	Salmon with dark purple mottling	Light salmon orange with light fringe of dark purple
Type of growth	Uniform medium-heavy growth of aerial hyphae	Uniform medium-heavy growth of aerial hyphae	Uniform medium-heavy growth of aerial hyphae	Uniform light growth of aerial hyphae
Topography	Level—no furrows	Level except furrows between sectors and parent, and few radial wrinkles near center	Level except hint of radial furrowing	Level—no furrows
Rudiments of perithecia	None	None	Few, very small	None

smooth with no rudiments of perithecia produced. Variations on other media are shown in table VI.

A24, on Brown's medium, showed no variation except at 30° C. where there was no growth. Growth was of the appressed type with very little aerial hyphae in the center, the color was seashell pink, and rudiments of perithecia were lacking. Variations on other media are shown in table VII.

A43, on Brown's medium, was identical with A17 described above, except that there was very slight growth at 20° C. Variations on other media are shown in table VIII.

TABLE V (Continued)

A 17–1	Richards' pH 4.5	Leonian's pH 4.8	Potato-dextrose pH 5.8	Coons' pH 6.5
		20° C.		
Color upper surface	Orange pink	Alizarine pink with narrow circle of dark purple around center	White to pale pink	Orange with light fringe of dark purple
Color reverse	Orange pink	Carmine mottled with apricot buff	White to pale pink	Light salmon orange with dark purple border
Type of growth	Uniform light growth of aerial hyphae	Uniform medium-heavy growth of aerial hyphae	Extremely slight growth, appressed	Uniform light growth of aerial hyphae
Topography	Deep concentric furrow, large wrinkles, very uneven border	Shallow concentric furrow; 8–10 short radial furrows near center	Level	Level—no furrows
Rudiments of perithecia	None	None	Very few	Very few
		25° C.		
Color upper surface	Salmon color	Alizarine pink with salmon center	Onion-skin pink	La France pink, some dark purple in border
Color reverse	Apricot buff	Carmine red slightly mottled with apricot buff	Buff pink	Same as above
Type of growth	Uniform light growth of aerial hyphae	Uniform medium-heavy growth of aerial hyphae	Appressed except light growth of aerial hyphae in center, border, and furrows	Appressed except few aerial hyphae in center and border
Topography	Shallow concentric furrow, 12–14 radial furrows	Shallow concentric furrow near center; 6–12 short radial furrows	Shallow concentric furrow or none; 5–10 short to long radial furrows	Level, no furrows
Rudiments of perithecia	None	None	None	None

TABLE V (Continued)

A 17–1	Richards' pH 4.5	Leonian's pH 4.8	Potato-dextrose pH 5.8	Coons' pH 6.5
		30° C.		
Color upper surface	Salmon color	Flesh pink	Orange pink	Orange pink; sector—La France pink with traces of deep blue in dark purple border
Color reverse	Apricot buff	Light salmon orange with slight carmine mottling	Apricot buff	Orange pink; sector—same with slight traces of dahlia purple and dark blue
Type of growth	Light growth of aerial hyphae, lighter in center	Uniform medium-heavy growth of aerial hyphae	Uniform light growth of aerial hyphae	Appressed except few aerial hyphae in center and covering sector
Topography	Level except numerous short radial furrows in the lobed margin	Level—no furrows	Level—no furrows	Level—no furrows
Rudiments of perithecia	None	None	None	None

A35, on Brown's medium, varied only in color at the different temperatures. At 18° and 20° C., the color was seashell pink, at 25° it was salmon-buff, with the reverse seashell pink, and at 30° orange pink with safrano pink reverse. The growth type was appressed and no rudiments of perithecia were formed. Variations on other media are shown in table IX.

A35–1 produced only the appressed type of growth on Brown's medium, except at 20° C., where there was no growth. The color varied from seashell pink at 18°, through salmon buff with seashell buff reverse at 25°, to light salmon orange with orange pink reverse at 30°. The surface was smooth and no rudiments of perithecia were formed. Variations on other media are recorded in table X. B 5 and B 5–1 will be discussed later in this paper.

TABLE VI

VARIATION IN MACROSCOPIC CHARACTERS OF A4 GROWN ON VARIOUS MEDIA AT DIFFERENT TEMPERATURES

A 4	Richards' pH 4.5	Leonian's pH 4.8	Potato-dextrose pH 5.8	Coons' pH 6.5
		18° C.		
Color upper surface	Flesh color mottled with Indian lake and having very wide border of dark purple	Dark purple with wide rose pink border; sector—dusky auricula purple	Seashell pink center, carmine border, remainder dark purple with slight mottling of seashell pink	Salmon pink center, remainder dark purple with slight mixture of salmon buff
Color reverse	Salmon with dahlia purple mottling, very wide border of dark purple	Same as above	Same as upper, but apricot buff instead of seashell pink	Same as above
Type of growth	Uniform medium-heavy growth of aerial hyphae	Medium-heavy growth of aerial hyphae; sector—light growth of aerial hyphae	Center and spots of medium-heavy growth of aerial hyphae, remainder light growth	Uniform light growth of aerial hyphae
Topography	Level—except few shallow wrinkles near center	Very shallow concentric furrow; uneven margin	Very shallow concentric furrow, and large shallow wrinkles	Some short radial furrows, very uneven margin
Rudiments of perithecia	Very few	Very numerous	Very numerous	Very few
		20° C.		
Color upper surface	Flesh color slightly mottled with Indian lake and having dark purple fringe	Center and wide border rose pink; between, wide uneven band of dark purple	Salmon pink center, carmine border, remainder dark purple with very slight mottling of seashell pink	Salmon buff center and dark purple border
Color reverse	Salmon with dahlia purple mottling and dark purple fringe	Same as above but carmine instead of rose pink	Same as upper but apricot buff instead of seashell pink	Same as above
Type of growth	Uniform light growth of aerial hyphae	Uniform medium-heavy growth of aerial hyphae	Light growth of aerial hyphae with ring of very light growth around center	Uniform light growth of aerial hyphae
Topography	Entire surface deeply wrinkled	Shallow concentric furrows; 8–10 short radial furrows near center	Very shallow concentric furrow, very shallow large wrinkles	Level—no furrows
Rudiments of perithecia	Numerous	Numerous	Very numerous	Very few

TABLE VI (Continued)

A 4	Richards' pH 4.5	Leonian's pH 4.8	Potato-dextrose pH 5.8	Coons' pH 6.5
		25° C.		
Color upper surface	Salmon	Center and border flesh pink; between, dark purple mottled with flesh pink	One plate orange-pink with radiate splashes of dark purple; one plate orange-pink, dark purple mottled; secant—⅓ size of plate, apricot buff	Salmon-buff with wide border of dark purple
Color reverse	Salmon	Same as upper, but carmine instead of flesh pink	Apricot buff with dark purple mottling	Salmon color with dark purple border
Type of growth	Only very light growth of aerial hyphae; mostly appressed	Felt-like growth of aerial hyphae	Uniform light growth of aerial hyphae; secant—very light growth of aerial hyphae	Uniform light growth of aerial hyphae
Topography	Entire surface deeply wrinkled	Shallow concentric furrow; some large wrinkles	Very shallow concentric furrow; hint of radial furrows or large wrinkles; no wrinkles in secant	Level—hint of concentric furrow
Rudiments of perithecia	None	Numerous	None	None

In general with strain A, media seemed to be responsible for greater variation in a given culture than temperature. Growth was greatest on Leonian's agar, decreasing in amount on potato-dextrose agar, Richards', Coons', to Brown's medium, where the development was least. Brown ('26) found the optimum pH for growth in his *Fusarium* species to lie toward the acid end. This is in agreement with the work here on *Gibberella Saubinetii.*

All cultures tended to produce the appressed type of growth, or with few aerial hyphae in the center on Brown's medium. Through the series the amount of aerial hyphae increased with

TABLE VI (Continued)

A 4	Richards' pH 4.5	Leonian's pH 4.8	Potato-dextrose pH 5.8	Coons' pH 6.5
		30° C.		
Color upper surface	Apricot buff; sectors (2), daphne pink	Chatenay pink	Orange pink	Orange pink with light fringe of dark purple
Color reverse	Apricot buff; sectors (2), dahlia purple	Light salmon orange with slight carmine mottling	Cinnamon rufous	Orange pink
Type of growth	Appressed mostly; very slight growth of aerial hyphae; sectors—light growth of aerial hyphae	Uniform medium-heavy growth of aerial hyphae	Uniform medium-heavy growth of aerial hyphae	Very light growth of aerial hyphae
Topography	Entire surface deeply wrinkled	20 or more shallow radial furrows	Shallow concentric circle near center; 25–30 shallow to deep radial furrows	Level except for very slight wrinkling in center
Rudiments of perithecia	None	None	None	None

the amount of growth, being greatest on Leonian's agar as is shown in pl. 10, fig. 4.

Rudiments of perithecia were not produced on Brown's medium at any temperature, but developed on all other media at 18° and 20° C., and on Leonian's at 25° C. also. Lower temperatures seemed to favor development of more numerous and larger perithecial rudiments. Tschudy ('37) observed that species of *Chaetomium* do not develop normal perithecia on peptone media. Abundant primordia would form on the surface of the agar but would develop no further. The fact that mature perithecia developed on agar alone showed the peptone to be an inhibiting factor. The addition of 2 per cent alcohol to the sterilized nutrient agar had the same inhibiting effect on the development of perithecia as the peptone. In this investigation on *Gibberella Saubinetii,* larger and more numerous

TABLE VII

VARIATION IN MACROSCOPIC CHARACTERS OF A 24 GROWN ON VARIOUS MEDIA AT DIFFERENT TEMPERATURES

A 24	Richards' pH 4.5	Leonian's pH 4.8	Potato-dextrose pH 5.8	Coons' pH 6.5
		18° C.		
Color upper surface	Flesh color mottled with Indian lake; very wide border of dark purple	Dark purple with wide rose pink border	Seashell pink center, border carmine, remainder dark purple with slight mottling of seashell pink	Salmon buff center, remainder dark purple with slight mixture of salmon buff
Color reverse	Salmon with dahlia purple mottling and dark purple border	Dark purple with Vandyke red border	Same as upper except apricot buff instead of seashell pink	Same as above
Type of growth	Uniform medium-heavy growth of aerial hyphae	Uniform medium-heavy growth of aerial hyphae	Center and spots of medium-heavy growth of aerial hyphae; remainder light growth	Uniform light growth of aerial hyphae
Topography	Few shallow wrinkles near center	Concentric furrow, few short radial furrows, lobed margin	Very shallow concentric furrow, and large shallow wrinkling	Some short radial furrows, very uneven margin
Rudiments of perithecia	Very few	Very numerous	Very numerous	Very few
		20° C.		
Color upper surface	Flesh color mottled with Indian lake; dark purple margin	Center and wide border rose pink; wide uneven band of dark purple between	Seashell pink center, carmine border, remainder dark purple with very slight mottling of seashell pink	No growth
Color reverse	Salmon with dahlia purple mottling and dark purple border	Same as upper but carmine instead of rose pink	Same as upper but apricot buff instead of seashell pink	No growth
Type of growth	Uniform light growth of aerial hyphae	Uniform medium-heavy growth of aerial hyphae	Uniform light growth of aerial hyphae except ring of very light aerial hyphae around center	No growth
Topography	Entire surface deeply wrinkled	Level—no furrows, uneven margin	Very shallow concentric furrow, hint of radial furrows near center	No growth
Rudiments of perithecia	Numerous	Numerous	Very numerous	None

TABLE VII (Continued)

A 24	Richards' pH 4.5	Leonian's pH 4.8	Potato-dextrose pH 5.8	Coons' pH 6.5
		25° C.		
Color upper surface	Salmon	Center and border flesh pink, remainder dark purple mottled with flesh pink	Seashell pink center; remainder dark purple mottled with seashell pink; dahlia purple traces in border	Salmon buff, wide border of dark purple
Color reverse	Salmon	Same as upper but carmine instead of flesh pink	Same as upper but cinnamon rufous instead of seashell pink	Salmon color with dark purple border
Type of growth	Mostly appressed; very slight uniform growth of aerial hyphae	Felt-like growth of aerial hyphae	Uniform light growth of aerial hyphae	Uniform light growth of aerial hyphae
Topography	Entire surface deeply wrinkled	Very shallow concentric furrow; 10 very shallow radial furrows; uneven margin	Very shallow concentric furrow, hint of radial furrows or large wrinkles	Level, except one very shallow concentric furrow around center
Rudiments of perithecia	None	Numerous	None	None
		30° C.		
Color upper surface	Apricot buff	No growth	White	Light salmon orange
Color reverse	Apricot buff	No growth	White	Light salmon orange
Type of growth	Appressed, mostly very slight growth of aerial hyphae	No growth	Appressed extremely light growth	Appressed
Topography	Entire surface deeply wrinkled	No growth	Level	Level except few shallow wrinkles in center
Rudiments of perithecia	None	No growth	None	None

TABLE VIII

VARIATION IN MACROSCOPIC CHARACTERS OF A43 GROWN ON VARIOUS MEDIA AT DIFFERENT TEMPERATURES

A 43	Richards' pH 4.5	Leonian's pH 4.8	Potato-dextrose pH 5.8	Coons' pH 6.5
		18° C.		
Color upper surface	Flesh color mottled with Indian lake, very wide border of dark purple	Dark purple with wide rose pink border; sectors (2), old rose with claret brown apices	Seashell pink center, carmine border, remainder dark purple with slight mottling of seashell pink	Salmon buff center, remainder dark purple with slight mixture of salmon buff
Color reverse	Salmon with dahlia purple mottling, wide border of dark purple	Dark purple with Vandyke red border; sectors (2), same as for upper surface	Same as upper but apricot buff instead of seashell pink	Same as above
Type of growth	Uniform medium-heavy growth of aerial hyphae	Uniform medium-heavy growth of aerial hyphae; sectors, light growth of aerial hyphae	Center and spots of medium-heavy growth of aerial hyphae, remainder light growth	Uniform light growth of aerial hyphae
Topography	Level, no furrows	Concentric furrow, few short radial furrows, much-lobed margin	Very shallow concentric furrow, large shallow wrinkling	Some short radial furrows, very uneven margin
Rudiments of perithecia	Very few	Very numerous	Very numerous	Very few

perithecial rudiments were produced on Leonian's medium, a peptone agar, than on other media employed. It has been stated previously that no fertile perithecia have been observed in strains A and B.

The color and color patterns varied widely with the different media used, and to a less extent with the temperature. With the decrease in temperature the colors became uniformly darker, usually red and dark purple. A deeper pigmentation was developed at 18° and 20° C. (see pl. 11). This agrees with the work of Crabill ('15) on production of pigmentation in *Coniothyrium,* but accords only in part with the statement of

TABLE VIII (Continued)

A 43	Richards' pH 4.5	Leonian's pH 4.8	Potato-dextrose pH 5.8	Coons' pH 6.5
		20° C.		
Color upper surface	Flesh color slightly mottled with Indian lake, dark purple fringed border	Center and wide border rose pink, remainder wide uneven band of dark purple	Seashell pink center, light carmine border, remainder dark purple with slight mottling of seashell pink	Salmon buff center, dark purple border
Color reverse	Salmon with dahlia purple mottling and dark purple fringed border	Same as upper but carmine instead of rose pink	Same as upper but apricot buff instead of seashell pink	Same as above
Type of growth	Uniform light growth of aerial hyphae	Uniform medium-heavy growth of aerial hyphae	Uniform light growth of aerial hyphae except ring of very light aerial hyphae around center	Uniform light growth of aerial hyphae
Topography	Deeply wrinkled near center, more shallow toward margin	Shallow concentric furrow, uneven margin	Very shallow concentric furrow, very large shallow wrinkles	Level, no furrows
Rudiments of perithecia	Numerous	Numerous	Very numerous	Very few

Ashley, Hobbs, and Roistrick ('37) that the optimum temperature for development and pigmentation in *Gibberella Saubinetii* is 24° C. Horne and Mitter ('27) found the intensity of coloring in some *Fusarium* species to be associated with a high C:N ratio. Snyder ('33) observed that the pH value, as well as the high carbohydrate content of the medium, may influence pigmentation. "The color of the mycelium" as stated in Gäumann-Dodge ('28, p. 233) "is largely dependent on the nutrition, especially on the reaction of the substrate.—The red mycelium of *Gibberella Saubinetii* on alkaline media becomes yellow on acid." In the present investigation, strain A became yellow on Richards' medium (pH 4.5) but red and purple on Leonian's (pH 4.8) and potato-dextrose agar (pH 5.8). On

TABLE VIII (Continued)

A 43	Richards' pH 4.5	Leonian's pH 4.8	Potato-dextrose pH 5.8	Coons' pH 6.5
		25° C.		
Color upper surface	Salmon	Center and border flesh pink, remainder dark purple mottled with flesh pink	Orange pink with radiate splashes of dark purple	Salmon buff, wide border of dark purple
Color reverse	Salmon	Same as upper but carmine instead of flesh pink	Cinnamon rufous with radiate splashes of dark purple	Salmon with wide border of dark purple
Type of growth	Mostly appressed, only very slight uniform growth of aerial hyphae	Felt-like growth of aerial hyphae	Uniform medium-heavy growth of aerial hyphae	Uniform light growth of aerial hyphae
Topography	Entire surface deeply wrinkled	Level except radial furrows in the lobed margin	Very shallow concentric furrow, hint of radial furrows or large wrinkles	Level, no furrows
Rudiments of perithecia	None	Numerous	None	None
		30° C.		
Color upper surface	Apricot buff	Chatenay pink	Apricot buff	Light salmon orange
Color reverse	Apricot buff	Apricot buff very deeply mottled with carmine	Apricot buff	Apricot buff
Type of growth	Mostly appressed, very slight growth of aerial hyphae	Uniform medium-heavy growth of aerial hyphae	Appressed except light growth of aerial hyphae in center and furrows	Extremely light growth of aerial hyphae
Topography	Entire surface deeply wrinkled	Shallow concentric circle near center, 10–12 shallow radial furrows	Level except 18–20 shallow radial furrows	Level except very shallow wrinkling in center
Rudiments of perithecia	None	None	None	None

TABLE IX

VARIATION IN MACROSCOPIC CHARACTERS OF A 35 GROWN ON VARIOUS MEDIA AT DIFFERENT TEMPERATURES

A 35	Richards' pH 4.5	Leonian's pH 4.8	Potato-dextrose pH 5.8	Coons' pH 6.5
		18° C.		
Color upper surface	Flesh color mottled with Indian lake, dark purple border	Dark purple with wide rose pink border	Seashell pink center, carmine border, remainder dark purple slightly mottled with seashell pink	Salmon buff center, remainder dark purple with slight mixture of salmon buff
Color reverse	Salmon with dahlia purple mottling and dark purple fringed border	Dark purple with Vandyke red border	Same as upper but apricot buff instead of seashell pink	Same as above
Type of growth	Uniform medium-heavy growth of aerial hyphae	Uniform medium-heavy growth of aerial hyphae	Center and spots medium-heavy growth of aerial hyphae, remainder light growth	Uniform light growth of aerial hyphae
Topography	Level, no furrows	Concentric furrow, few short radial furrows, lobed margin	Very shallow concentric furrow, and wide shallow wrinkles	Same short radial furrows, very uneven margin
Rudiments of perithecia	Few, small	Very numerous	Very numerous	Very few
		20° C.		
Color upper surface	Flesh color mottled with Indian lake, dark purple fringed border	Center and wide border rose pink, wide uneven band of dark purple between	Whitish to very pale pink	Salmon buff center, remainder dark purple
Color reverse	Salmon with dahlia purple mottling, dark purple fringed border	Same as upper but carmine instead of rose pink	Same as above	Same as above
Type of growth	Uniform light growth of aerial hyphae	Uniform medium-heavy growth of aerial hyphae	Very slight development, appressed except for few aerial hyphae	Uniform light growth of aerial hyphae
Topography	Surface deeply wrinkled in center, more shallow toward margin	Very shallow concentric furrow, hint of radial furrows, uneven margin	Level, no furrows	Level, no furrows
Rudiments of perithecia	Numerous	Numerous	None	Very few

TABLE IX (Continued)

A 35	Richards' pH 4.5	Leonian's pH 4.8	Potato-dextrose pH 5.8	Coons' pH 6.5
		25° C.		
Color upper surface	Salmon slightly mottled with deep slate violet	Center and border flesh pink, remainder dark purple mottled with flesh pink	Orange pink with radiate splashes of dark purple	Salmon buff with wide border of dark purple
Color reverse	Salmon slightly mottled with dull dusky purple	Same as upper but carmine instead of flesh pink	Cinnamon rufous with radiate splashes of dark purple	Salmon with dark purple border
Type of growth	Uniform light growth of aerial hyphae	Felt-like growth of aerial hyphae	Uniform medium-heavy growth of aerial hyphae	Uniform light growth of aerial hyphae
Topography	Entire surface deeply wrinkled	Shallow concentric furrow, large wrinkles somewhat radial, uneven margin	Very shallow concentric furrow, hint of radial furrows or large wrinkles	Very shallow concentric furrow near center, or none
Rudiments of perithecia	None	Numerous	None	None
		30° C.		
Color upper surface	Apricot buff	Chatenay pink	Flesh color	Grenadine
Color reverse	Apricot buff	Apricot buff very deeply mottled with carmine	Apricot buff	Grenadine pink
Type of growth	Mostly appressed, very slight growth of aerial hyphae	Uniform medium-heavy growth of aerial hyphae	Heavy growth of aerial hyphae	Light growth of aerial hyphae
Topography	Entire surface deeply wrinkled	8–12 very shallow radial furrows	1 deep concentric furrow near margin, about 12 radial furrows	1 concentric furrow, remainder wrinkled and somewhat warty
Rudiments of perithecia	None	None	None	None

TABLE X

VARIATION IN MACROSCOPIC CHARACTERS OF A 35-1 GROWN ON VARIOUS MEDIA AT DIFFERENT TEMPERATURES

A 35-1	Richards' pH 4.5	Leonian's pH 4.8	Potato-dextrose pH 5.8	Coons' pH 6.5
18° C.				
Color upper surface	Bittersweet pink	Bordeaux with few apricot buff aerial hyphae in center	Chestnut with radiating broken lines of ox-blood red	Orange pink
Color reverse	Orient pink	Bordeaux	Burnt sienna	Orange pink
Type of growth	Appressed	Appressed	Appressed	Appressed
Topography	Shallow wrinkles over entire surface	Level, no furrows	Level, no furrows	Some short radial furrows, very uneven margin
Rudiments of perithecia	None	None	None	None
20° C.				
Color upper surface	Light salmon orange	Bordeaux with few apricot buff aerial hyphae in center	Light buff	Orange pink
Color reverse	Orange pink	Bordeaux	Light buff	Orange pink
Type of growth	Appressed	Appressed	Appressed, very light growth	Appressed
Topography	Shallow wrinkles toward center	Very shallow concentric furrow	Level, no furrows	Level, no furrows
Rudiments of perithecia	None	None	None	None

Coons' (pH 6.5) and Brown's (pH 5.6) the strain was very pale pink to colorless. The hydrogen-ion concentration of the media was taken only at the beginning of the experiment before inoculations had been made, and it is quite probable that substances produced by the fungus during growth on certain media tend to neutralize some of the acid, thus producing the red color. A correlation between rate of growth and pigmentation

TABLE X (Continued)

A 35-1	Richards' pH 4.5	Leonian's pH 4.8	Potato-dextrose pH 5.8	Coons' pH 6.5
		25° C.		
Color upper surface	Salmon orange	Bordeaux	Cinnamon rufous with broken radiate lines of dahlia purple	Salmon buff
Color reverse	Apricot buff	Bordeaux	Same as above	Pale flesh color
Type of growth	Appressed	Appressed	Appressed	Appressed
Topography	Very shallow concentric furrow	Very shallow concentric furrow	Very shallow concentric furrow	Level, no furrows
Rudiments of perithecia	None	None	None	None
		30° C.		
Color upper surface	Orange chrome	Brick red	Flesh color	No growth
Color reverse	Medium salmon orange	Hay's russet	Apricot buff	No growth
Type of growth	Appressed	Appressed	Light growth of aerial hyphae	No growth
Topography	Level, no furrows	Level, no furrows	About 12–13 shallow radial furrows	No growth
Rudiments of perithecia	None	None	None	No growth

in *Alternaria Solani* was pointed out by Bonde ('29). The maximum for both was at 25–30° C.

Variations as referred to in the previous paragraphs are not of a permanent nature, as was shown in subsequent transfers to other media. They are the non-heritable changes due to environment, the "eco-variants" of Dickinson ('32).

A total of nine sectors was formed in six of the 360 plates used in this investigation, five being on Leonian's agar at 18° C., one on potato-dextrose agar at 25° C., one on Coons' medium at 30° C., and two on Richards' medium at 30° C. Distribution of sectors according to cultures, media, and temperature are shown in table XI.

TABLE XI
DISTRIBUTION OF SECTORS ACCORDING TO CULTURES, MEDIA, AND TEMPERATURES

Cultures	Number of sectors	Medium	Temperature
A4	1	Leonian's	18° C.
A4	1	potato-dextrose	25° C.
A4	2	Richards'	30° C.
A17–1	2	Leonian's	18° C.
A17–1	1	Coons'	30° C.
A43	2	Leonian's	18° C.

In an attempt to isolate these possible saltants, inocula were taken from the apex, center, and outer edge of each sector and transferred to fresh media. A transfer of the part not sectoring was made at the same time, for comparison. Only the two sectors from A17–1 on Leonian's agar at 18° C. proved to be of a different form from the parent culture. These variants, designated as A17–1–1 and A17–1–2, were identical in appearance. They will be discussed further under the next topic.

B 5 and B 5–1 produced no sectors, islands, or other visible modifications when grown on the different media at different temperatures. B 5–1, on all media and at all temperatures, was lighter in color than the corresponding culture of B 5. The colors ranged from ox-blood red to Eugenia red except on Brown's medium, where it was light buff or pale pinkish buff to white. Depth of color increased with decrease in temperature.

The B series, like the A series previously mentioned, did not grow well on Brown's medium, the growth ranging from none (B 5 at 20° C.) through 1 cm. (B 5–1 at 20° C.) to covering the surface of the medium at higher temperatures. No rudiments[7] of perithecia were formed on this medium.

On all other media and at all temperatures used, the aerial growth filled the Petri plate. No rudiments of perithecia were

[7] The term "perithecial rudiments" has been used, because up to this time no mature ascospores had been found. One mature perithecium of B 5 on Leonian's agar at 18° C. was found when serial sections were cut.

produced at 30° C. Distribution at all other temperatures is shown in table XII.

TABLE XII

DISTRIBUTION OF PERITHECIAL RUDIMENTS ACCORDING TO MEDIA AND TEMPERATURE

Media	Strain or variant	25° C.	20° C.	18° C.
Coons'	B 5	Numerous	Very numerous	Very numerous
	B 5–1	None	Very few	Very few
Richards'	B 5	None	Numerous	Numerous
	B 5–1	None	None	None
Potato-dextrose	B 5	Numerous	Very numerous	Very numerous
	B 5–1	None	None	Numerous
Leonian's	B 5	Numerous	Very numerous	Very numerous
	B 5–1	None	Numerous	Numerous

Vasudeva ('30) found that certain strains of *Fusarium* when grown on shallow plates of an acid phosphate medium readily gave rise to strangely diverging sectors. Many of these sectors did not prove to be variants and were therefore termed "false sectors." Matsuura ('32) observed that temperature and composition of the nutrient media influence the frequency of mutation, being greater on potato decoction agar. Stakman, Christensen, Eide, and Peturson ('29) have shown there were more numerous variations in *Ustilago Zeae* on some media than on others and that they occur at comparatively high temperatures. However, Tu ('30) was unable to induce permanent variations in species of *Fusarium* by subjecting them to different media and incubating them at various temperatures. Brown ('26, '28) reported that saltations in *Fusarium* were more frequent on concentrated Richards' solution agar than on many other media. This was confirmed by Chaudhuri ('31). Christensen ('26) observed more numerous mutations in strains of *Helminthosporium* on one media than on another under similar conditions. In 1937 he and Davies demonstrated the frequency of mutation of *Helminthosporium* on a bacteria-staled medium.

One race cultured for seventeen years produced eighty-one varieties from seventeen colonies on the bacteria-staled medium, while on the same number of colonies on potato-dextrose agar none was produced. Paxton ('33) was able to secure consistent mutations in *Helminthosporium sativum* on Czapek's medium, with the $NaNo_3$ omitted. An average of five sectors in each plate was observed. On Czapek's medium which was used as a check, very few sectors were formed. Chaudhuri ('31) found that the greater number of variants would revert to the original form when grown on some medium or when returned to the original host. He considered saltation in fungi to be purely a nutritive phenomenon, unless it be a rare case of true mutation. Coons and Larmer ('30) obtained variants of *Cercospora beticola* in cultures on artificial media. They regarded them as modified forms with nutritional disturbances playing a role in their development. Caldis and Coons ('26) expressed the same opinion for variants in *Colletotrichum* and *Cladosporium*. This disturbance might have been due to the connections with the substratum being severed by the drying of the mycelium, or the variant might have arisen from cells the protoplasm of which had been poisoned or had been affected by some other unknown factor.

Chodat ('26) favored the premutation theory of de Vries as an explanation for the appearance of variants in the various media. His belief was that the media did not produce the variants but only made visible the pre-existing mutations. Shear and Wood ('13) found it impossible to trace any causal relation or connection between most of the phenomena of variation observed in *Glomerella* and the conditions of environment to which the cultures were subjected.

Induced variation by heating the ascospores of *Eurotium* was reported by Barnes ('28, '31). Some of these variants had remained stable over a period of about four years. He suggested that, apart from the probable nuclear changes, a general derangement of the physiological balance of the cell may be responsible for variation. Dickson ('32) and Goldring ('36) were unable to obtain any variants by this method. Chris-

tensen ('29), and later Mitra ('31), observed that certain lines of *Helminthosporium* species mutate only at the higher temperatures for growth. Christensen found the optimum temperature for mutations to be 25–27° C., while Mitra noted that it was 30° C. In the present investigation on *Gibberella Saubinetii,* more variations appeared at 18° C. than at the three higher temperatures, as is shown in table XI.

F. Constancy of Mycelial and Conidial Forms.—In the present investigations, also in *Fusarium* studies carried on by Brown ('28), sectors were formed which were mycelial in character and produced few or no conidia. At other times in mycelial types, sectors have been formed with very numerous conidia and very little aerial mycelium. On A17–1, a sector of A17, no conidia developed when transferred to fresh potato-dextrose agar and grown at room temperature as described earlier in this paper. A17, although mycelial in character, produced many conidia under the same conditions.

A17 and A17–1 were grown on five different media and at four different temperatures as described in the preceding experiment, and the macroscopic characters are represented in tables IV and V. They were examined microscopically to determine the constancy of these forms under various cultural conditions. These results are given in table XIII.

Inocula from the two sectors of A17–1 were transferred to fresh potato-dextrose agar in Petri plates. A transfer of inoculum of A17–1 was made at the same time for comparison. A17–1–1 and A17–1–2 remained the typical sector color, or perhaps the color was slightly deeper. The upper surface was Eugenia red to Vandyke red and the reverse was apricot buff to acajou red. The mycelium was mostly appressed, with very little aerial hyphae, and was somewhat wet in appearance. The surface was smooth except for one (rarely two) concentric furrows and numerous short shallow radial furrows. These cultures were definitely of the conidial type. A17–1 remained a mycelial type and produced no condia on potato-dextrose agar at room temperature.

TABLE XIII

PRODUCTION OF CONIDIA IN LINES A17 AND A17-1 UNDER VARIED ENVIRONMENTAL CONDITIONS.

Temperature	Richards'	Potato-dextrose	Leonian's	Coons'	Brown's
A 17 (mycelial form producing numerous conidia):					
18° C.	Many	Few	Few	Many	Few
20° C.	Many	Very few	Very few	Few	None
25° C.	Very many	Few	Few	Few	Very few
30° C.	Very many	Few	Very few	Very few	Very, very few
A 17–1 (mycelial form producing no conidia):					
18° C.	Very few	None	None, except on 2 sectors where numerous	None	None
20° C.	Very few	Very few	None	None	None
25° C.	Few	Very few	None	1 plate—many 1 plate—very few	None
30° C.	Very few	Very few	None	None	Very few

Inocula from A17–1–1 and A17–1–2 were transferred to potato-dextrose agar in test-tubes. Instead of the appressed conidial form again, an aerial form was produced. It was pale pinkish and powdery in appearance, and microscopic examination showed numerous conidia.

Attempts to Induce the Pionnotal Stage to Revert to the Aerial Mycelial Stage

In cultural work with species of *Fusarium,* variants have developed which were in the form of pionnotes.[8] However, so far the writer has been able to find no instance reported of a culture completely reverting to the aerial mycelial phase after it once had gone into the pionnotal phase. In this work A35–1

[8] Pionnotes is merely a biological term for an effuse conidial stage, with a maximum of conidia and a minimum of aerial mycelium, which, as a rule, is slimy when young and resin-like or powdery-dry in old age. (Wollenweber, '13.)

developed as an appressed form with very numerous conidia. When grown on various media at a rather wide range of temperatures, as described under "Attempts to Induce Variation," the growth was always appressed except on potato-dextrose agar at 30° C. where a light growth of aerial hyphae developed. At 20° C. on Leonian's agar the color of this culture was Bordeaux. When transfers were made to malt extract agar in tubes the color reverted to the light salmon orange characteristic of this culture on this medium, but the growth had a slimy appearance with no aerial mycelium. When examined microscopically, the growth was found to consist of a maximum of conidia, the pionnotal stage. A transfer to Leonian's agar made at the same time produced the Bordeaux color again, but the mycelium, instead of being completely appressed, was largely aerial. Conidia were very numerous and were 3- to 7- (mostly 5-) septate.

A subsequent transfer to potato-dextrose agar in a Petri plate produced a moderately heavy growth of aerial hyphae which were pink with a yellowish tint. This growth soon collapsed, and the color of the upper surface changed to Eugenia red and the reverse to acajou red to Vandyke red.

To learn whether the pionnotal phase would revert to the aerial mycelial phase, the series of transfers were made as shown in fig. 1. In each case, a small portion of mycelium was transferred with a sterile needle to the fresh media. The Roman numbers in fig. 1 represent the stages in the development of the aerial mycelial phase from the pionnotal phase, and are as follows:

I. Pionnotal (described previously in text).

II. Appressed type, salmon orange with very faint zoning of Eugenia red. Very numerous conidia.

III. Appressed type, salmon orange with Eugenia red center. Very numerous conidia.

IV. Wide zone of aerial hyphae about 1 cm. from the center, remainder appressed. Salmon orange except for a wide zone of irregular radially striped Eugenia red coinciding with the zone of aerial hyphae. Very numerous conidia.

V. Aerial mycelial stage. Aerial hyphae cottony, white to pale pink, reverse surface acajou red. Conidia fairly numerous.

VI. Dense aerial growth. Aerial hyphae cottony, white to slightly mottled with Eugenia red, substratum Eugenia red. Few or no conidia.

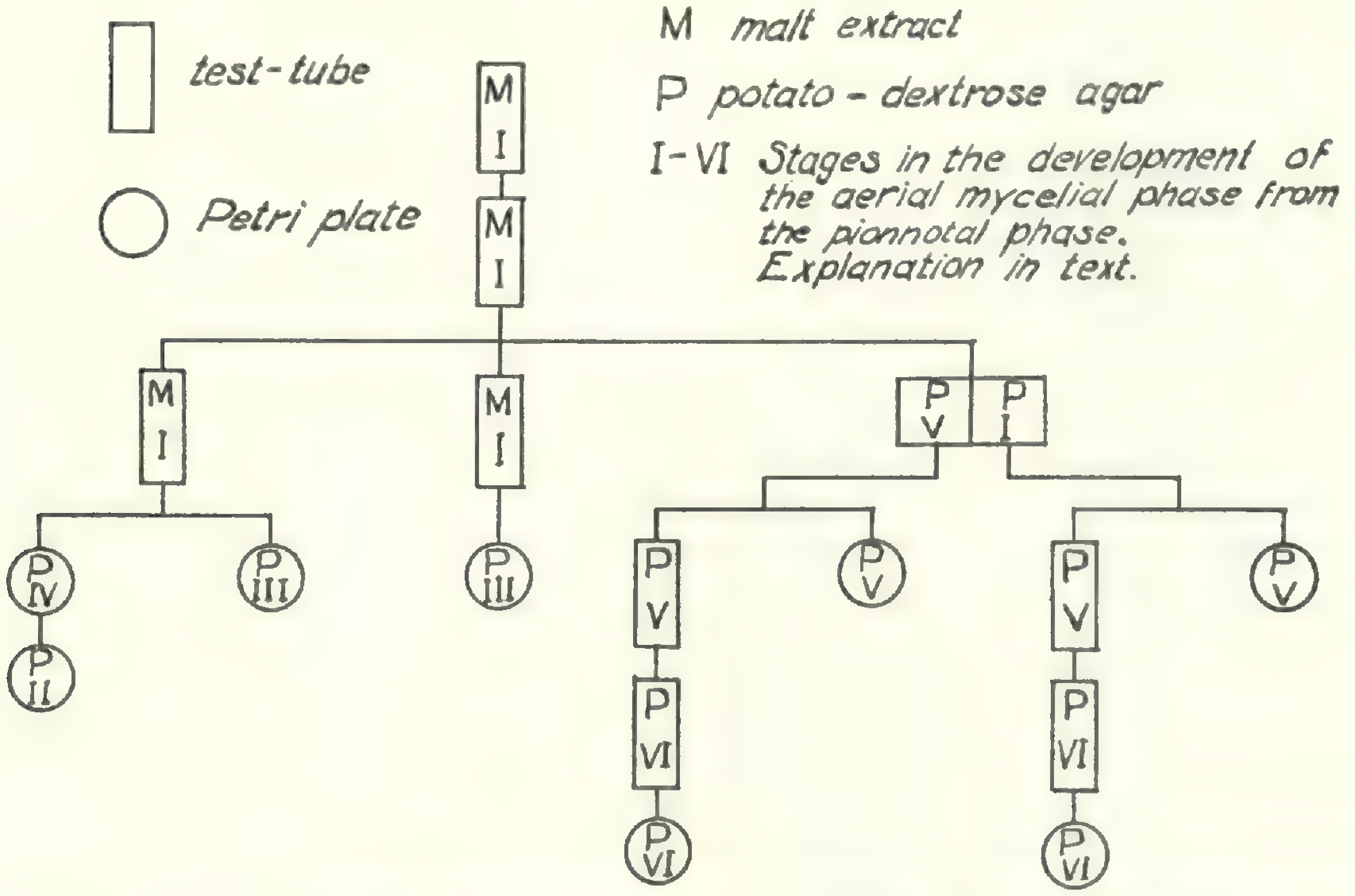

Fig. 1. Graphic representation of the development of the aerial mycelial phase from the pionnotal stage. The culture at the right in the third generation was of type I at first but later developed an area of type V.

In this series of cultures there seemed to be a transition from the pionnotal phase with no aerial hyphae (I) and the appressed type (II, III), through the aerial and appressed forms (IV), to the aerial mycelial forms (V, VI); from the orange color (I, II), through the orange and red (III, IV), to the red substratum (V, VI); from forms with a maximum or very numerous conidia (I, II, III, IV), through forms with fairly numerous conidia (V) to forms with few or no conidia (VI) (see pl. 12).

Observations on Sector Formation

Figure 2 shows the form and comparative distance from the inoculum of all variant sectors formed in an attempt to induce

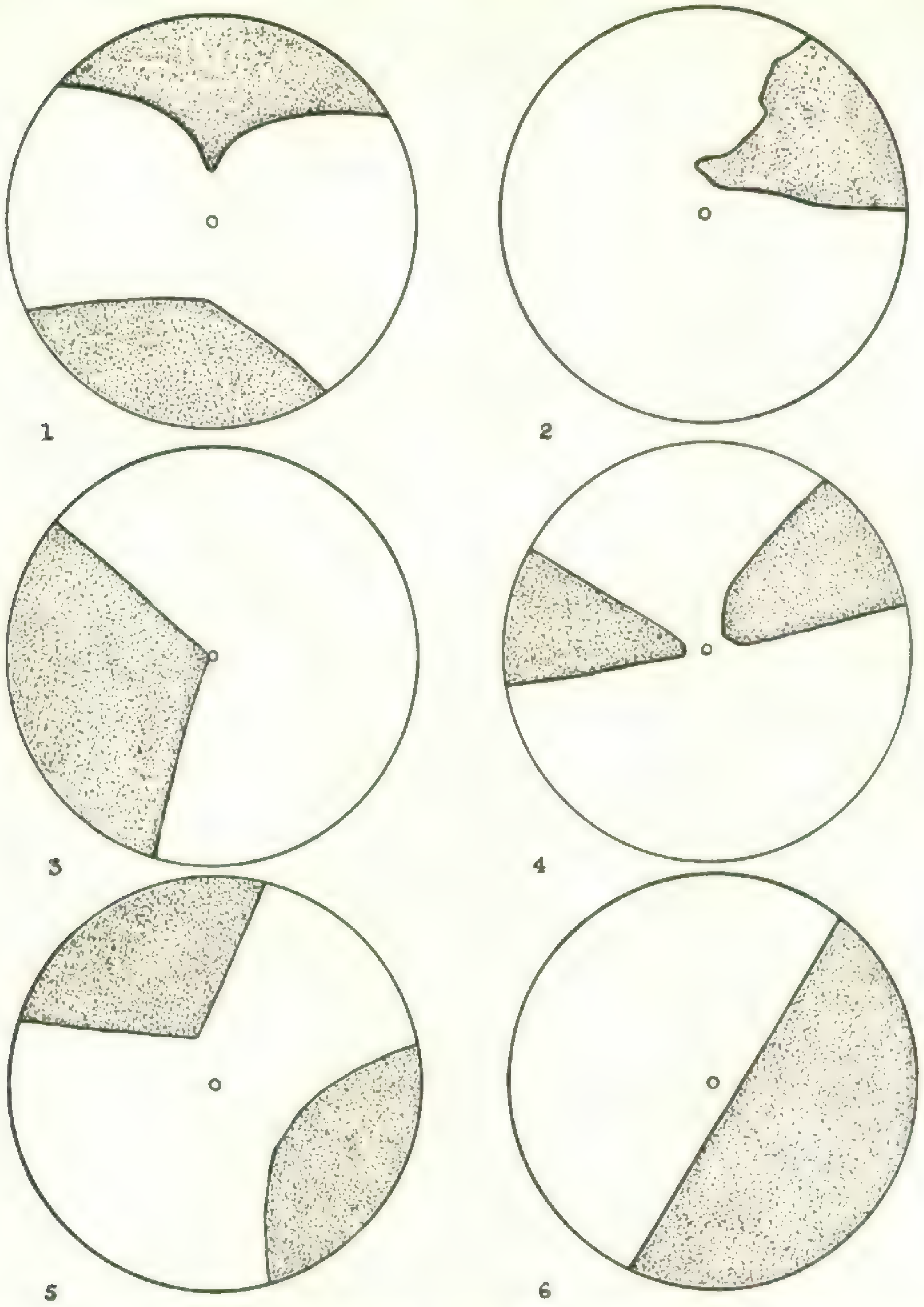

Fig. 2. Sectors formed in cultures grown at various temperatures on different media: *1*, A 17–1, on Leonian's agar at 18° C. One sector 15 mm. from inoculum, nearer one 8 mm. from inoculum; *2*, A 17–1, on Coons' agar at 30° C. Sector 4 mm. from inoculum; *3*, A 4, on Leonian's agar at 18° C. Sector starts at inoculum; *4*, A 4, on Richards' agar at 30° C. Both sectors start 3 mm. from inoculum; *5*, A 43, on Leonian's agar at 18° C. One sector 16 mm. from inoculum, nearer one 8 mm. from inoculum; *6*, A 4 on potato-dextrose agar at 25° C. Sector (secant) 3 mm. from inoculum.

variation by varying the temperature and medium. It can readily be seen that sectoring began at varying distances from the center or from the piece of inoculum. One sector (A 4 on Leonian's agar at 18° C.) started at the piece of inoculum and another (A 43 on Leonian's agar at 18° C.) started 8 and 16 mm. from the inoculum. In one, both sectors on the plate started at the same time, but in the other two cases one sector started at approximately twice the distance of the first sector from the inoculum. Christensen ('26) found that more sectors started near the edge of the colony than near the center in *Helminthosporium*. Brown ('26) found that more saltations took place near the center or in the older mycelia and that they occurred in irregular patches.

In a total of 360 Petri plates, six plates formed sectors. Of these, three plates formed two each, and three formed one each, making a total of nine sectors. The chance of getting a plate with one sector then is 9/360 or 1/40, and the chance of getting a plate with two sectors would be $1/40 \times 1/40$ or 1/1600. Yet in this experiment there were three plates with two sectors each, or 3/360 or 1/120.

The question then arises as to why there were so many cases of double sectors. In two sectors the growth type was observed to be the same in both; or if the sectors were differentiated on the basis of deeper or lighter pigmentation than the remainder of the culture, both showed this character; or if it were ability to produce conidia, both exhibited this character. It seems then that whatever factor or factors were operating to produce one sector tends to produce two. It acts in a qualitative as well as in a quantitative way.

Attempts to Produce Intermediate Strains by Crossing Two Morphologically Different Strains

Brierley ('29) suggested that certain recorded variations in fungi might be explained on the basis of the "mixochimaera" hypothesis. This term was used first by Burgeff ('14) for a mycelium in which nuclei and cytoplasm of distinct types were associated as the result of hyphal fusion.

Hyphal anastomoses are common in fungi. Ward ('88), Beauverie and Guillermond ('03), and Brierley ('22) have demonstrated anastomoses in *Botrytis.* Ezekiel ('24) observed fusions between hyphae of two varieties of *Sclerotinia americana* but no further growth. Matsumoto ('21) noted in *Rhizoctonia Solani* fusions between hyphae of the same or closely related strains; or strains which have recently originated from the same ancestral type. He was of the opinion that it was not a sexual process. Stevens ('22) reported that hyphal fusions were common in *Helminthosporium.* Dosdall ('23) and Christensen ('26) observed numerous fusions of germ tubes in *Helminthosporium,* Christensen noting as many as seven instances of lateral fusion in one series. Ocfemia ('24), in his work on *Helminthosporium,* showed figures of anastomoses very similar to those of the present author on *Gibberella Saubinetii* as shown in pl. 14. Drechsler ('23) noted in *Helminthosporium Bromi* the same type of fusion of germ tubes as did Christensen, but the former observed also that some of the hyphal fusions would swell into subglobose bodies and proliferate short irregular processes of inflated segments, the whole resulting in dark brown, knotty masses of mycelium. Some of these continued to increase in size, developing into subspherical sclerotia readily visible to the naked eye. He did not cultivate these further but was of the opinion that they represented immature perithecia.

Aside from these observations on hyphal anastomoses, there are the investigations of those who have studied hyphal fusions as such, or who have attempted to synthesize new types from pre-existing strains or even species. Burgeff ('14, '15) produced a neutral strain by mechanically mixing the cell contents of a plus and a minus hypha of *Phycomyces nitens.* This product, as previously mentioned, he termed "mixochimaera." Leonian ('30) attempted to induce mixochimaera in *Fusarium moniliforme* by growing two morphologically different types together in nutrient media, but no new strain was produced. However, Hansen and Smith ('32, '34, '35) reported that heterogenic types of *Botrytis cinerea* resulted from mixing

together two homogenic strains of the fungus in the same culture. Mixing of cell contents by anastomosis resulting in "heterocaryosis" was suggested as the mechanism of this phenomenon. Interspecific combinations were made in the same way by using two distinct species. The authors suggested that the production of these aberrant homotypes was due to gene changes brought about in some way by interspecific anastomosis.

Davidson, Dowding, and Buller ('32) used hyphal anastomosis as a character for differentiation of species of *Microsporum.* They observed fusions between mycelia of the same species but never between different species. Dickinson ('32) isolated fusion cells which were the product of the anastomosis of two contrasting strains of *Fusarium fructigenum.* On isolation from the subsequent growth of such fusion cells, the cultural characters of the two parent strains were found unchanged. Das Gupta's observations ('34) of hyphal anastomoses in *Diaporthe perniciosa* led him to suggest that the fusion of DH_C with DH_F mycelium exerted an influence on the latter and brought about the conversion of DH_F into DH_C mycelium.

The present work was undertaken, first, to find if hyphal anastomosis took place when conidia[9] from two contrasting strains of *Gibberella Saubinetii* were allowed to germinate on the same drop of nutrient agar (this procedure has been described under "Materials and Methods"); and second, to determine whether new and different strains were produced as a result of this fusion. The following combinations were made: A35–1 × B5–1; A35 × A35–1; and B5 × B5–1. Camera-lucida drawings of hyphal anastomoses are shown in pl. 14, figs. 1–8. Conidia of A35–1 and B5–1 were germinated separately on nutrient agar drops, and hyphal anastomoses occurred also in single spore colonies (pl. 14, figs. 9–11).

The agar drops with the germinated conidia were transferred to Petri plates of nutrient agar. In the first two combi-

[9] During several months in culture, A35 lost its capacity for production of conidia. Hyphal tips were substituted.

nations, there were sharp lines of demarcation between the two strains showing that each had inhibited the growth of the other. In the third combination the two colonies intermixed for the most part. Conidia were isolated along the line separating the two colonies, or along the surface where the two colonies overlapped. Of the total of 56 conidia isolated from the A35–1 × B5–1 combination, 31 produced the A35–1 type and 25 the B5–1 type. In the second combination, A35 × A35–1, 44 conidia were isolated and all exhibited the A35–1 type. Of the 55 conidia isolated from the third combination, B5 × B5–1, 28 were the B5 type and 27 the B5–1 type. No intermediate or new strain resulted from mixing the mycelia.

As can be seen from the data recorded, there was approximately a 1:1 ratio of the original types which appeared in the isolates from the mixed cultures of A35–1 × B5–1, and B5 ×B5–1. The occurrence of only one original type in the isolates from the "A35 × A35–1" cross may be explained by the supposition that A35, which was not producing conidia when the cross was made, still did not produce conidia. This evidence obtained from these crosses and re-isolations indicates that although hyphal anastomoses were common between the different pairs of variants, the strains remained separate.

Cytological Study

No intensive study of the whole cytological phenomenon in variants of *Gibberella Saubinetii* was attempted. However, observations were made of structures which proved to be perithecial rudiments; also of the nuclear condition in hyphal anastomoses.

An examination of the perithecial rudiments showed that the vast majority had not developed to maturity. One perithecium, nevertheless, which had been produced in a culture of B 5 on Leonian's agar at 18° C. was found to contain mature ascospores (pl. 13). The asci had probably already disintegrated, for the ascospores appeared to be loose in the perithecial cavity. The ascospores were 4-septate. Eide ('35) found them to be 3-septate in the strains which he examined.

Four-septate ascospores are exceptional in this species (Wollenweber and Reinking, '35).

In the study of hyphal anastomoses, the nuclear condition was found to be more complex than the data on isolation of single-spore colonies from the mixed cultures would lead one to suspect. Dickinson ('32) found the fusion cells in hyphae of *Fusarium fructigenum* to be binucleate, although both nuclei were sometimes found in one half of the cell. The hyphal cells are generally uninucleate except in the fusion cells, or sometimes in cells adjacent or very near to the fusion cells.

In this study, lateral processes were observed to push out from adjacent filaments and come together and fuse. The wall between them disintegrates, thus forming a connection between cells of the two filaments. Plates 15 and 16 show various nuclear conditions, many of which cannot be explained until some additional information has been gained. Figures 2 and 3 of pl. 15, and figs. 2a, 5a, 6a, and 7a of pl. 16 show binucleate fusion cells either before or after one nucleus has migrated into the other half of the cell, conditions described by Dickinson ('32, fig. 6) for *Fusarium fructigenum.* In other fusion cells one or both nuclei appear to have divided once or more, and in a few cases some of the daughter nuclei are seen migrating through the anastomosing tube (pl. 15, figs. 4, 5 and 7, pl. 16, figs. 1, 2b, 4, 5, 6b). D'Oliveira ('36, pls. 4 and 7) reported a similar phenomenon in *Fusicladium.* His figures showed anastomoses between two hyphae, and between two conidia. In the former, nuclei are seen which have recently divided, and in the latter some recently divided nuclei are seen passing into the anastomosing tube. No instance of caryogamy in these anastomoses was observed. All fusion cells were two- to several-nucleate.

Discussion and Conclusions

Gibberella Saubinetii appears to be a very variable species exhibiting a number of forms or phases differing from each other in type and rate of growth, color, and amount of conidial production. These characters may be influenced by media and

temperature. Brown ('26) remarks, with regard to *Fusarium fructigenum,* that "the tendency of these *Fusarium* strains to saltate is a function of the cultural medium." That the majority of variations recorded in this paper were due to reaction to the environment is evidenced by the return of the variants to the original form when grown under the original conditions of culture. Others, however, did not revert to the original form but continued to produce the same type of variation or to form still other variant types.

One culture, originating as a sector from A35, went through a cycle of growth phases. It was mentioned under "Sources of Cultures" that the original cultures used in this study were obtained from Dr. Eide, who had isolated them from corn stubble in 1932 and 1933. He described his original ascospore isolate A43–4–I, from which this A43–4–I–I or A line developed, as follows: "'Normal' type; characterized by abundant, cottony, aerial mycelium, red, often with a tinge of yellow. The bottoms of the cultures were pink to deep Eugenia red." (Eide '32, p. 12, table 4, and p. 13.) A43–4–I–I or A of this paper is described in detail on page 106, and is illustrated in pl. 9, fig. 1. Briefly, it was an orange pink form at first with scant aerial mycelium but with age produced abundant thick-walled deep purple cells in the substratum. Upon further culture, A35–1 was produced as a sector in one of the conidial isolates (table III). It differed from A35 in having no aerial mycelium and developed no deep purple thick-walled hyphae. It was of the conidial or sporulating type. On five different media and at four different temperatures it produced this appressed type of growth with very numerous conidia, but on potato-dextrose agar at 30° C. a light aerial growth resulted. When transferred from Leonian's agar at 20° C. to potato-dextrose agar and malt agar, the culture assumed the pionnotal phase. In subsequent transfers to potato-dextrose agar, as is shown in fig. 1, the pionnotal phase changed to the aerial mycelial phase with few or no conidia. This phase seems comparable to the description of Eide's original ascospore isolate, although a stock culture of the original could not be obtained for purposes of comparison.

Whether this culture will again pass from the aerial mycelial phase, through the appressed or conidial phase and the pionnotal phase, to the aerial mycelial phase again is still being investigated. Upon the basis of data obtained thus far it seems a more logical conclusion that there is a definite cycle of growth phases through which this fungus passes, than to conclude that all these variations represent separate strains within the species.

It has been definitely shown that the pionnotal phase reverts to the aerial mycelial phase. This, it seems, is a very significant contribution.

Summary

1. A number of conidial isolates of two strains of *Gibberella Saubinetii* were allowed to grow for several generations on potato-dextrose agar to determine the relative stability of the strains. Only one permanent variant was formed in one strain and two in the other strain.

2. Nine conidial isolates, including the three variants, were grown on Brown's, Coons', Richards', Leonian's, and potato-dextrose agar at 18°, 20°, 25°, and 30° C., to induce variations. Ecovariants, or temporary variants due to environment, as well as some permanent variations, were produced. More variations, temporary and permanent, occurred at the lower temperatures and on Leonian's agar. Growth also was best on Leonian's agar. The optimum temperature for growth was 25° C.

3. Mycelial and conidial forms were only fairly constant when subjected to variations in temperature and media. Numerous conidia appeared in sectors of the mycelial types which had previously formed no conidia; and conidial types have changed to aerial forms producing only very few or no conidia.

4. The pionnotal stage in one strain reverted to the aerial mycelial stage which seemed to answer the description of the original ascospore isolate from corn stubble. It completed a cycle of growth by passing from the aerial mycelial phase through the conidial and appressed phase, through the pionnotal phase back to the aerial mycelial phase.

5. No new or intermediate strains resulted from crossing two morphologically different strains. While nuclear migration occurred between hyphal anastomoses, there was no evidence that caryogamy took place in the hyphal anastomoses.

6. The two facts: (1) production of two sectors at about the same time, and (2) identical mutant sectors, favor the hypothesis that the saltation is somatic rather than germinal. The soma, rather than the germ-plasm, might more readily be expected to saltate more or less simultaneously at diverse points under the proper stimulus. Germinal changes are usually somewhat at random and even if two occurred in the same culture it might confidently be expected that they would be different mutants.

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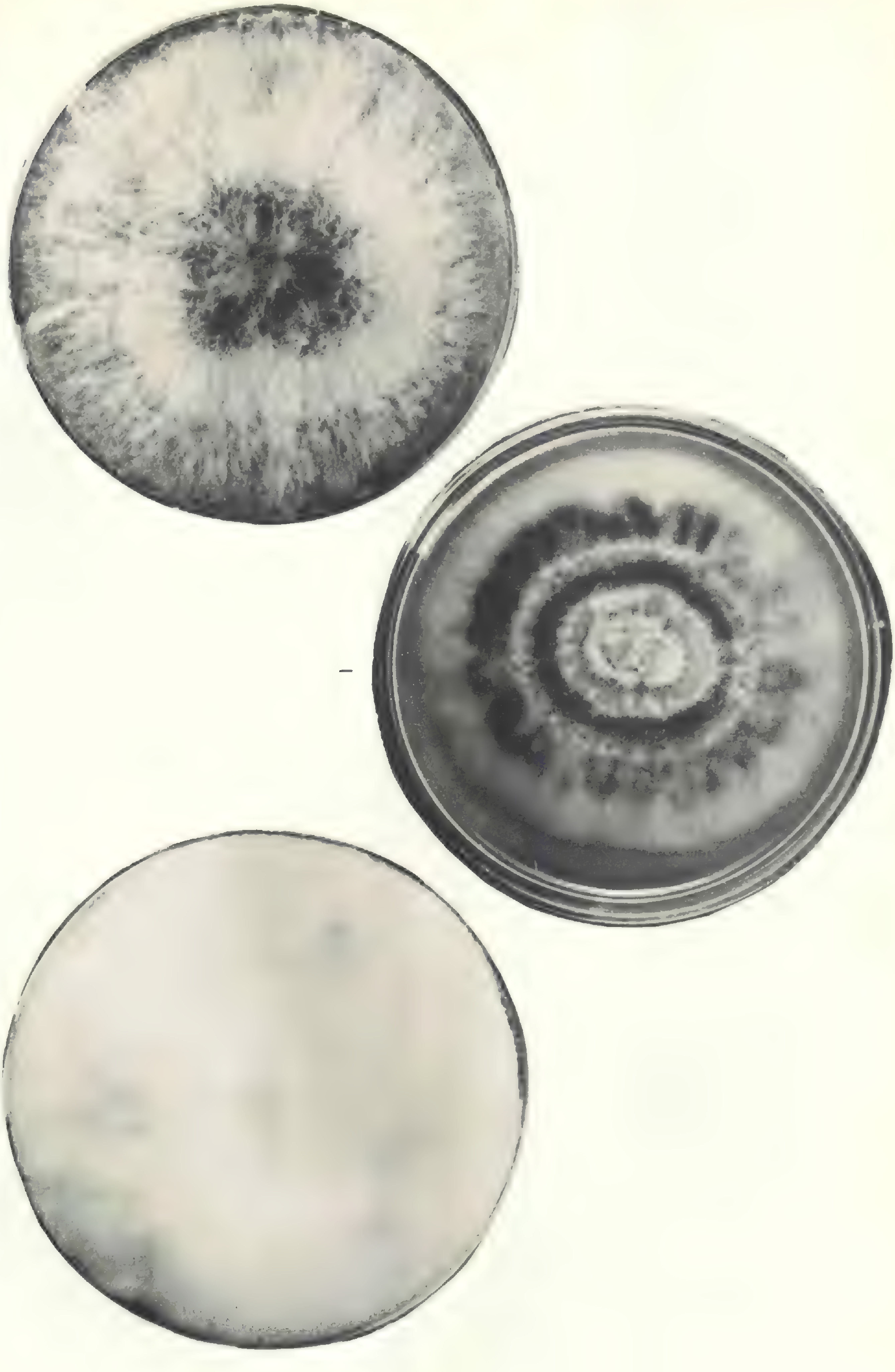
Explanation of Plate

PLATE 9

Cultures grown on potato-dextrose agar at room temperature.

Fig. 1. Petri plate culture of strain A.
Fig. 2. Petri plate culture of strain B.
Fig. 3. Petri plate culture of B 5–1, a variant from strain B (fig. 2).



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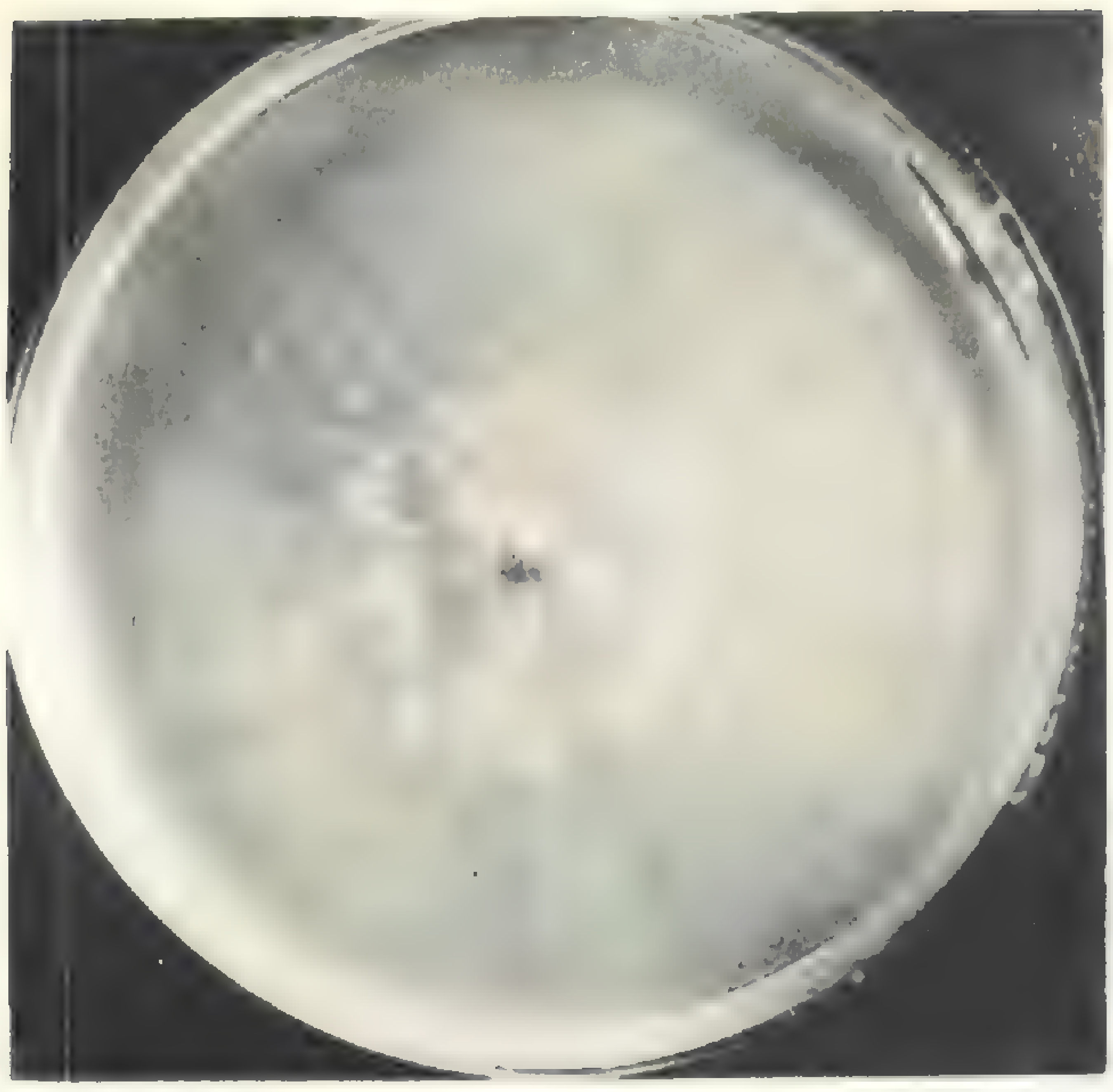
GODDARD—VARIATION IN GIBBERELLA SAUBINETII

Explanation of Plate

PLATE 10

Variations in a single culture due to differences in the composition of the medium. Temperature, 25° C.

Fig. 1. A 17 on Brown's agar.
Fig. 2. A 17 on Coons' agar.
Fig. 3. A 17 on Richards' agar.
Fig. 4. A 17 on Leonian's agar.
Fig. 5. A 17 on potato-dextrose agar.



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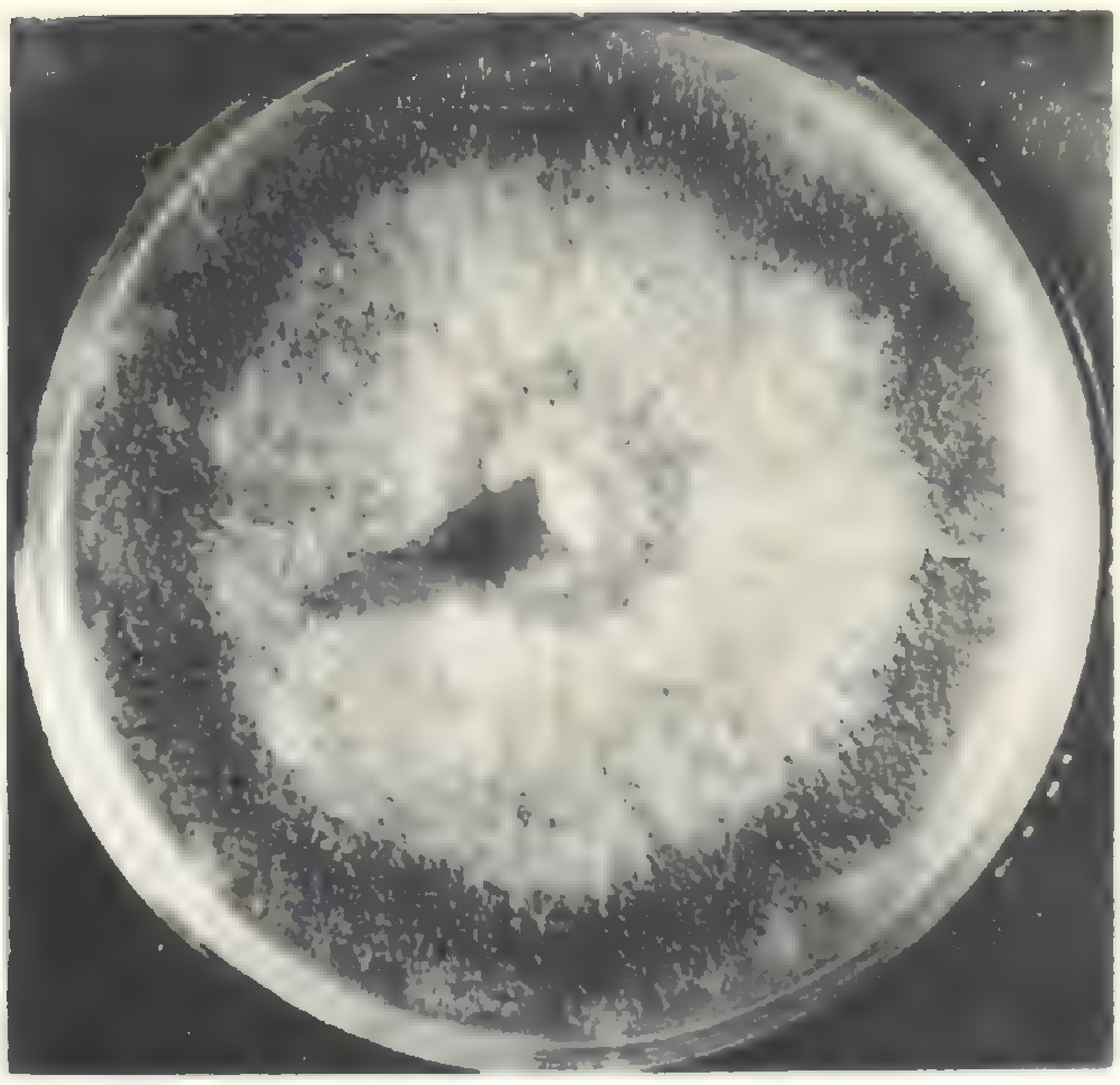

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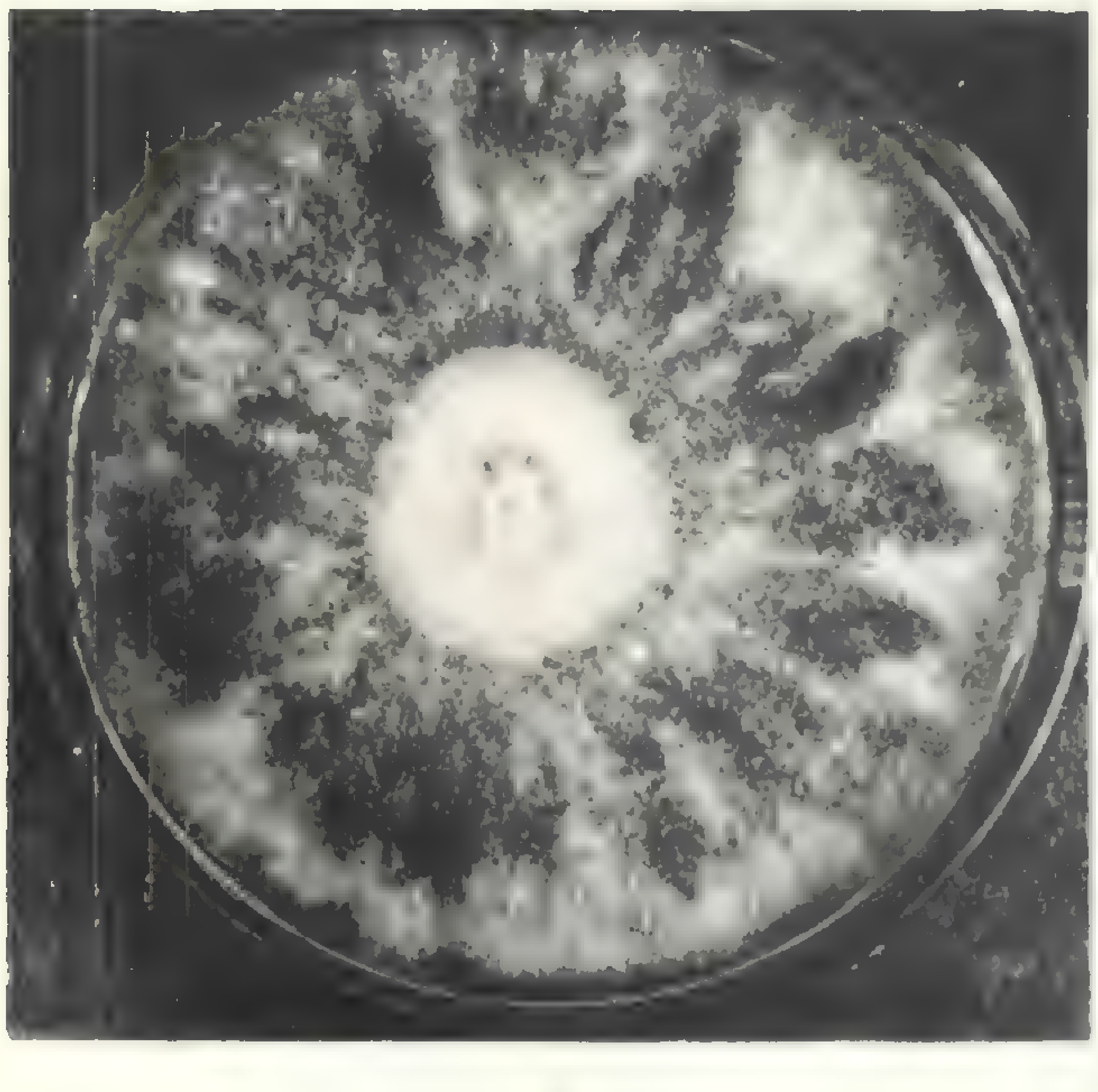

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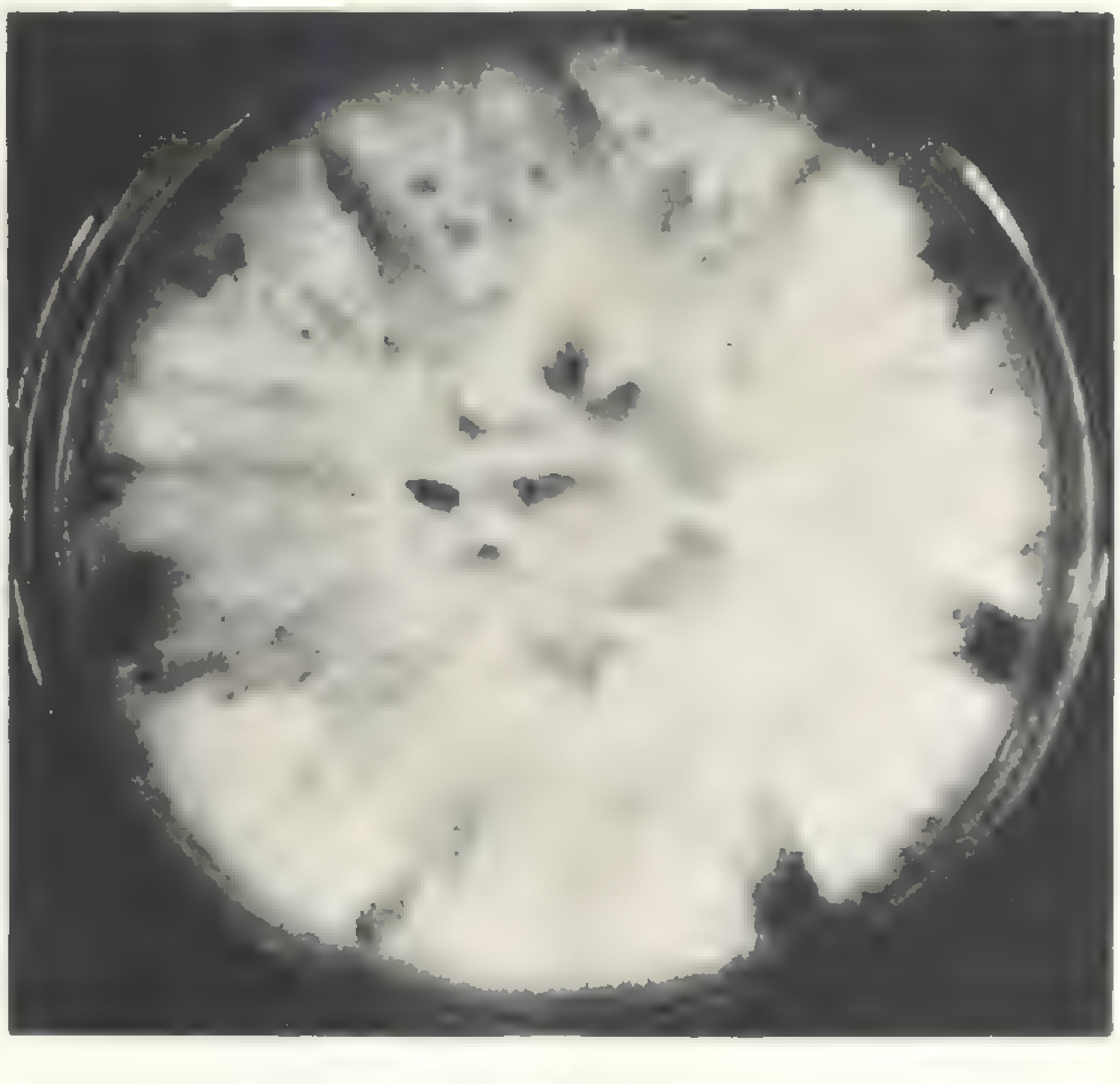

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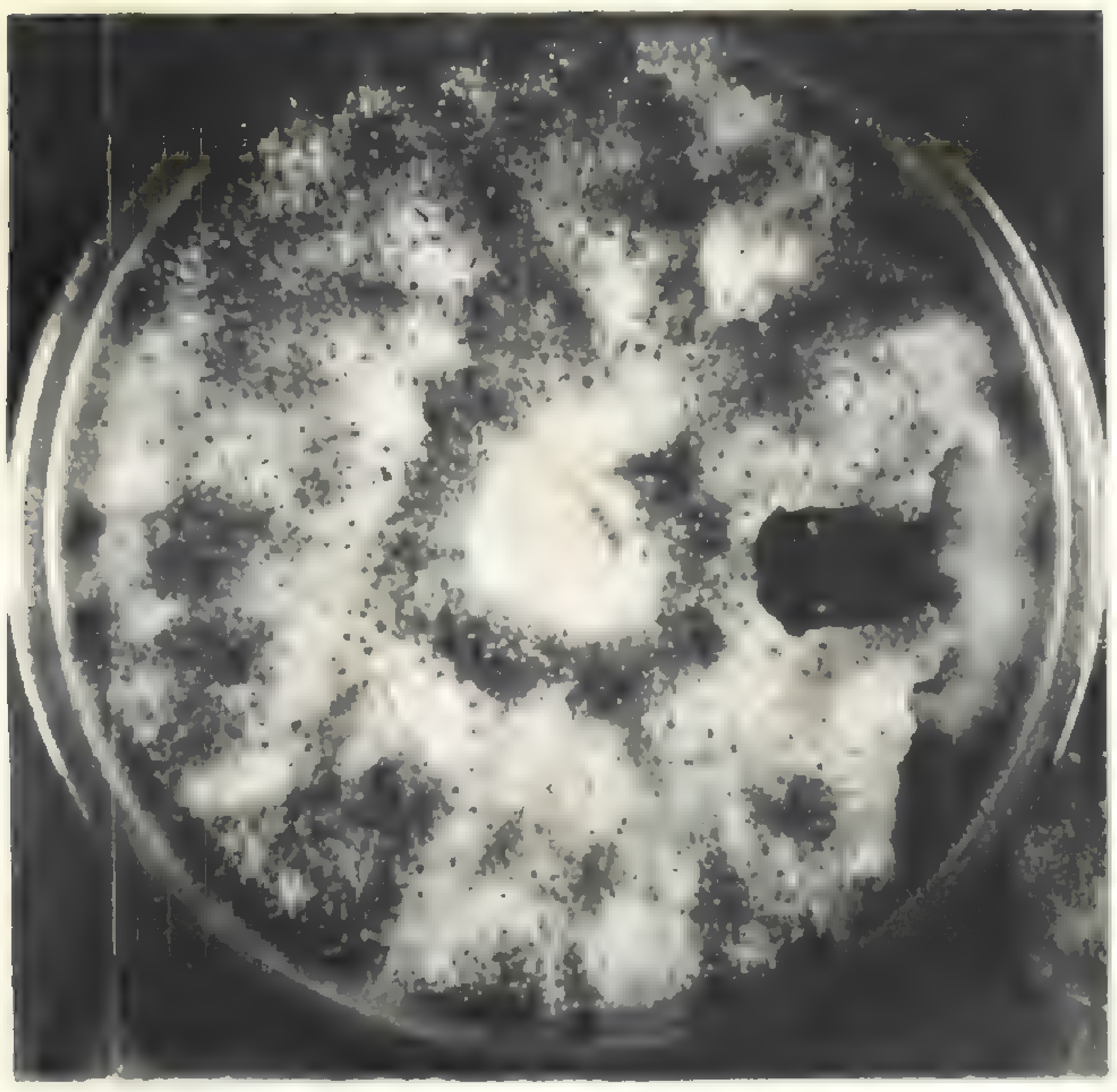
GODDARD—VARIATION IN GIBBERELLA SAUBINETII

Explanation of Plate

PLATE 11

Variations in a single culture due to differences in temperature. Grown on potato-dextrose agar.

Fig. 1. A 17 at 18° C.
Fig. 2. A 17 at 20° C.
Fig. 3. A 17 at 25° C.
Fig. 4. A 17 at 30° C.



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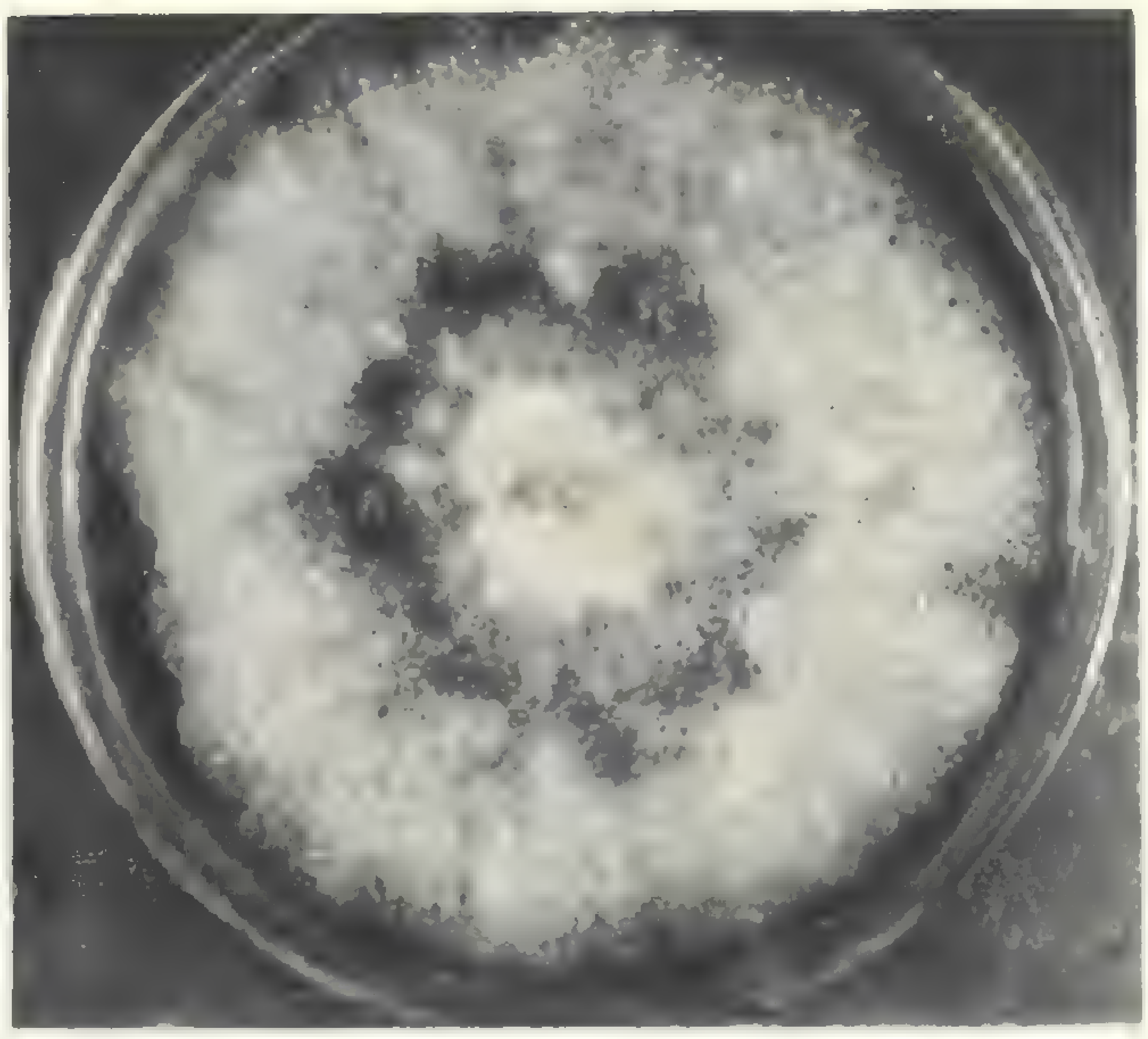

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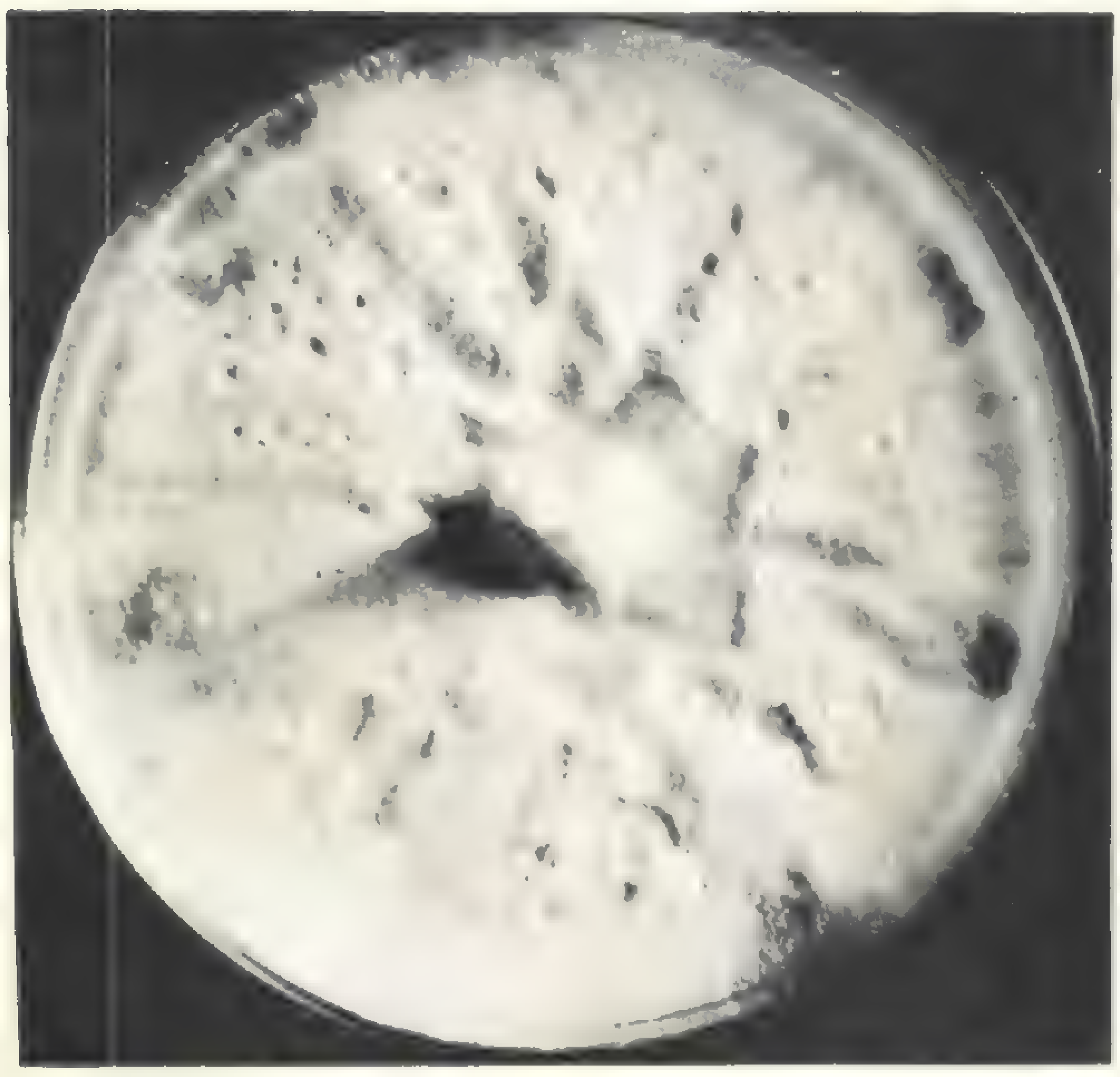

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GODDARD—VARIATION IN GIBBERELLA SAUBINETII

Explanation of Plate

PLATE 12

Culture A 35–1 on potato-dextrose agar, showing some stages in the development of the aerial mycelial phase from the pionnotal phase. Stage I, the pionnotal phase, was grown in test-tube cultures.

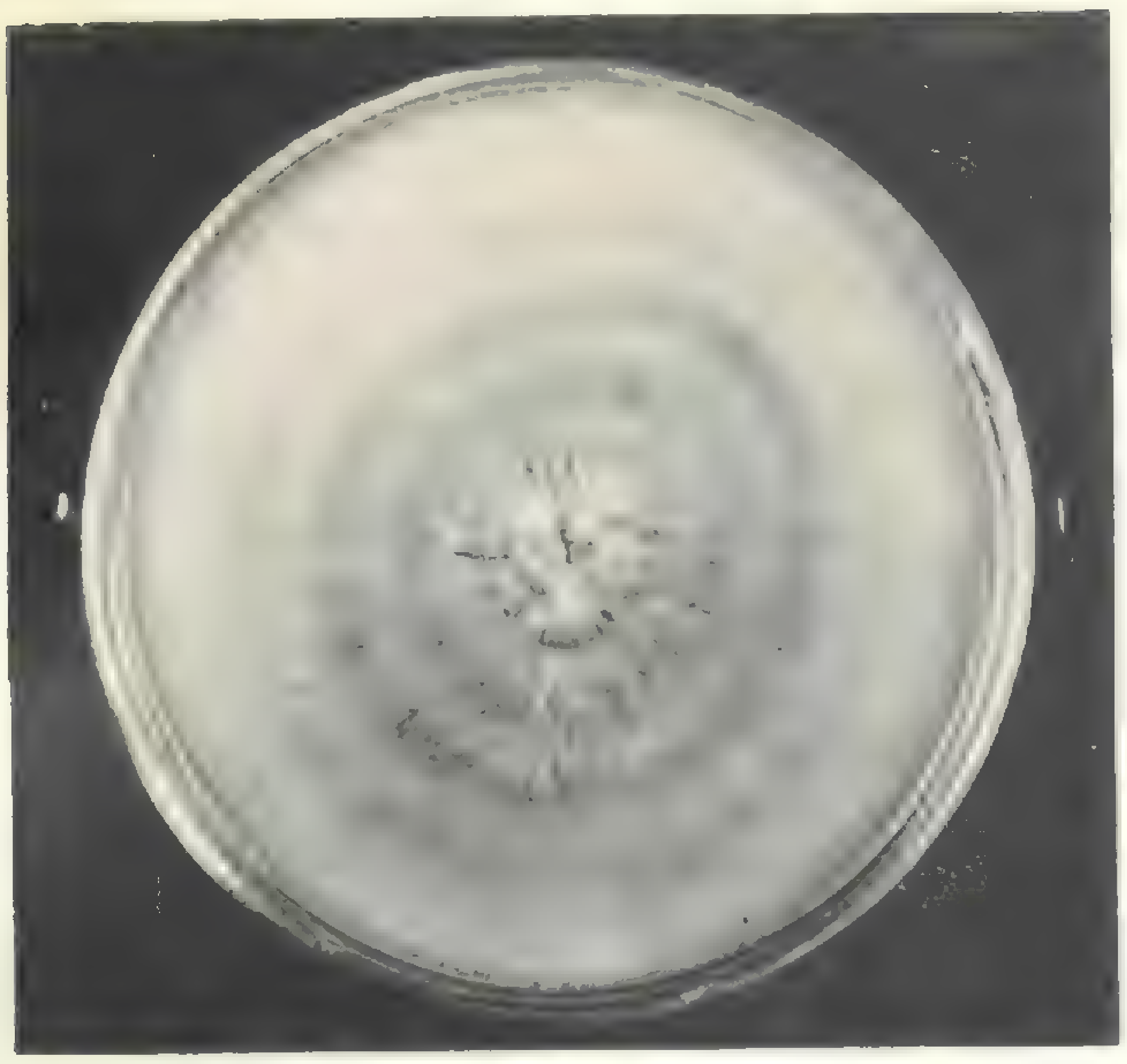
Fig. 1. Stage II. Appressed type, salmon orange with Eugenia red center; very numerous conidia.

Fig. 2. Stage III. Appressed type, salmon orange with Eugenia red center; very numerous conidia.

Fig. 3. Stage IV. Wide zone of aerial hyphae about 1 cm. from the center, remainder appressed; salmon orange except for a wide zone of irregular radially striped Eugenia red coinciding with the zone of aerial hyphae; very numerous conidia. This stage is intermediate between the appressed type and the aerial mycelial type. It was also intermediate in color between salmon orange and Eugenia red.

Stage V. was identical in appearance with Stage VI. Conidia were fairly numerous.

Figs. 4 and 5. Stage VI. Dense aerial mycelium; aerial hyphae cottony, white to slightly mottled with Eugenia red; few or no conidia (see fig. 1 in text). Fig. 5 is a culture developed from the pionnotal region of the test-tube culture, and fig. 4 from the aerial mycelium of the same culture. The two resultant cultures are identical.



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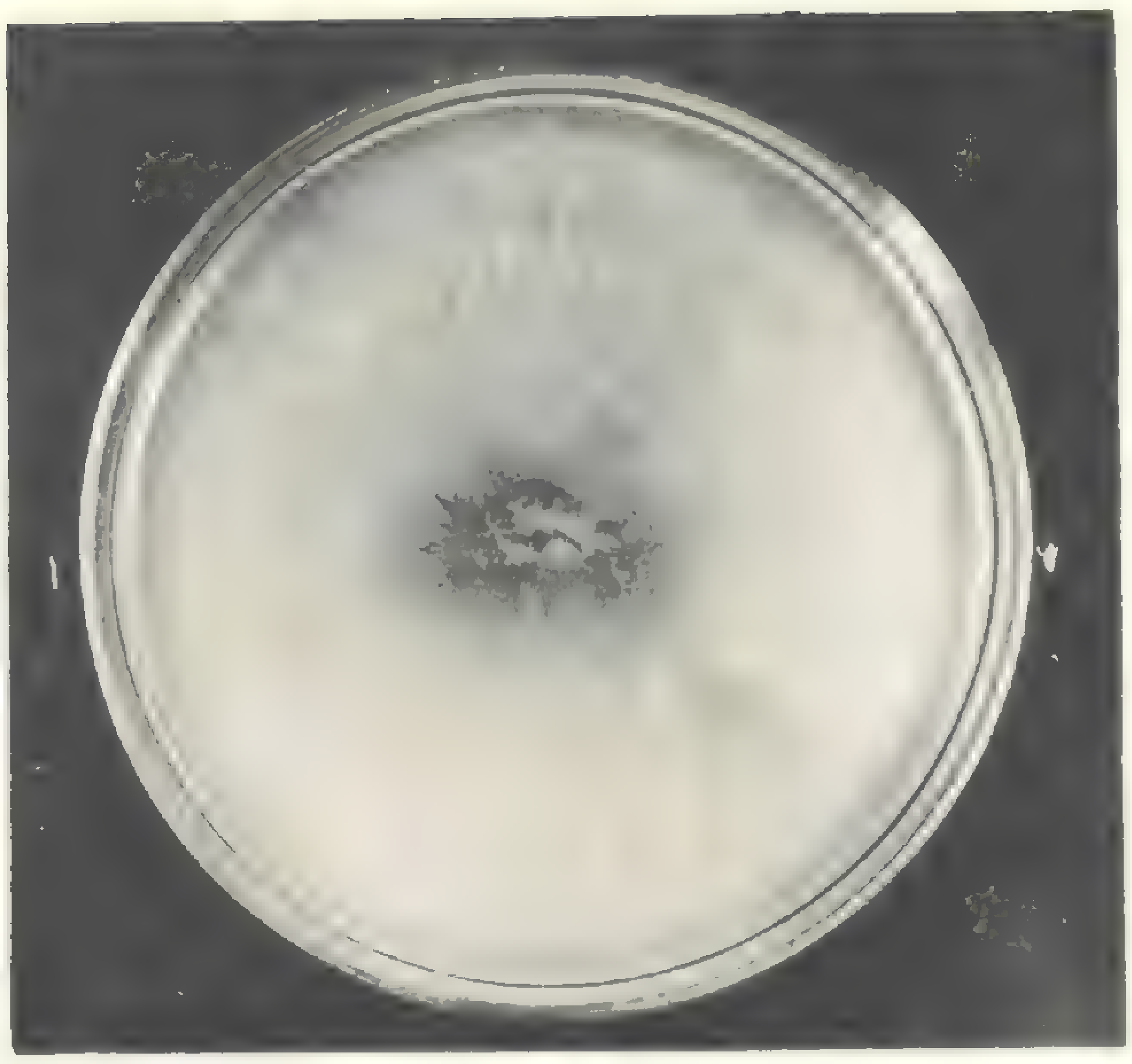

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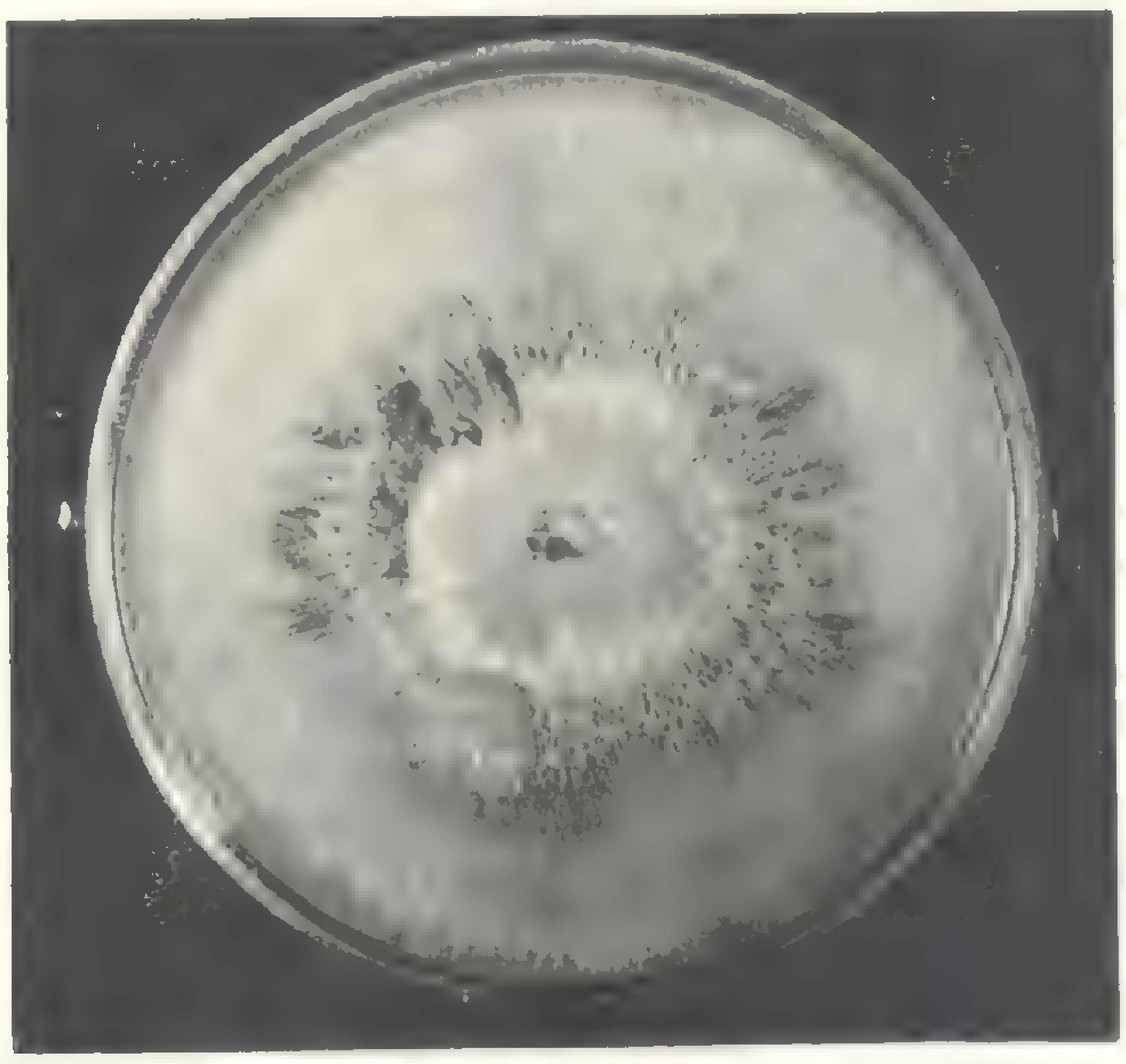

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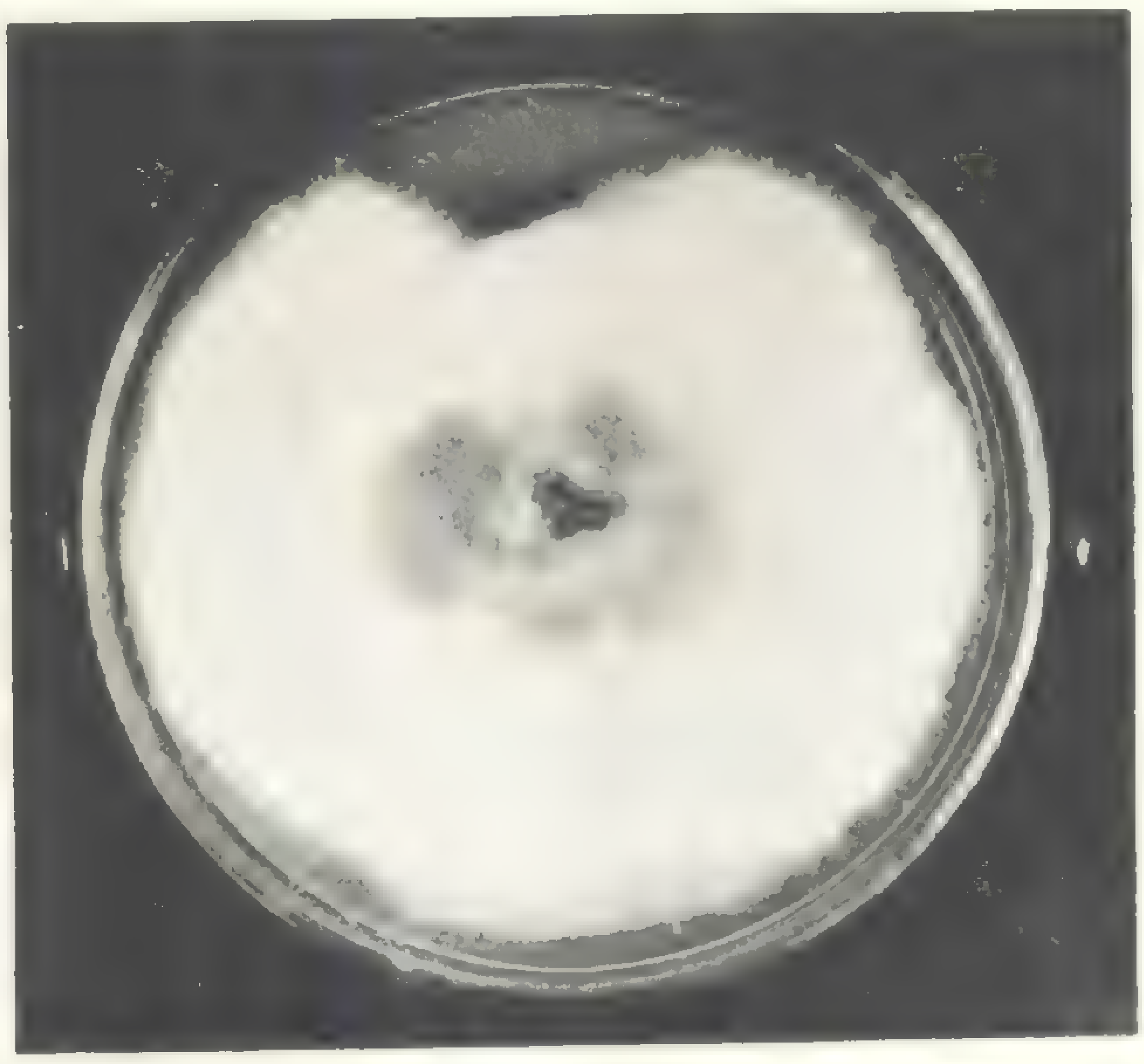

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GODDARD—VARIATION IN GIBBERELLA SAUBINETII

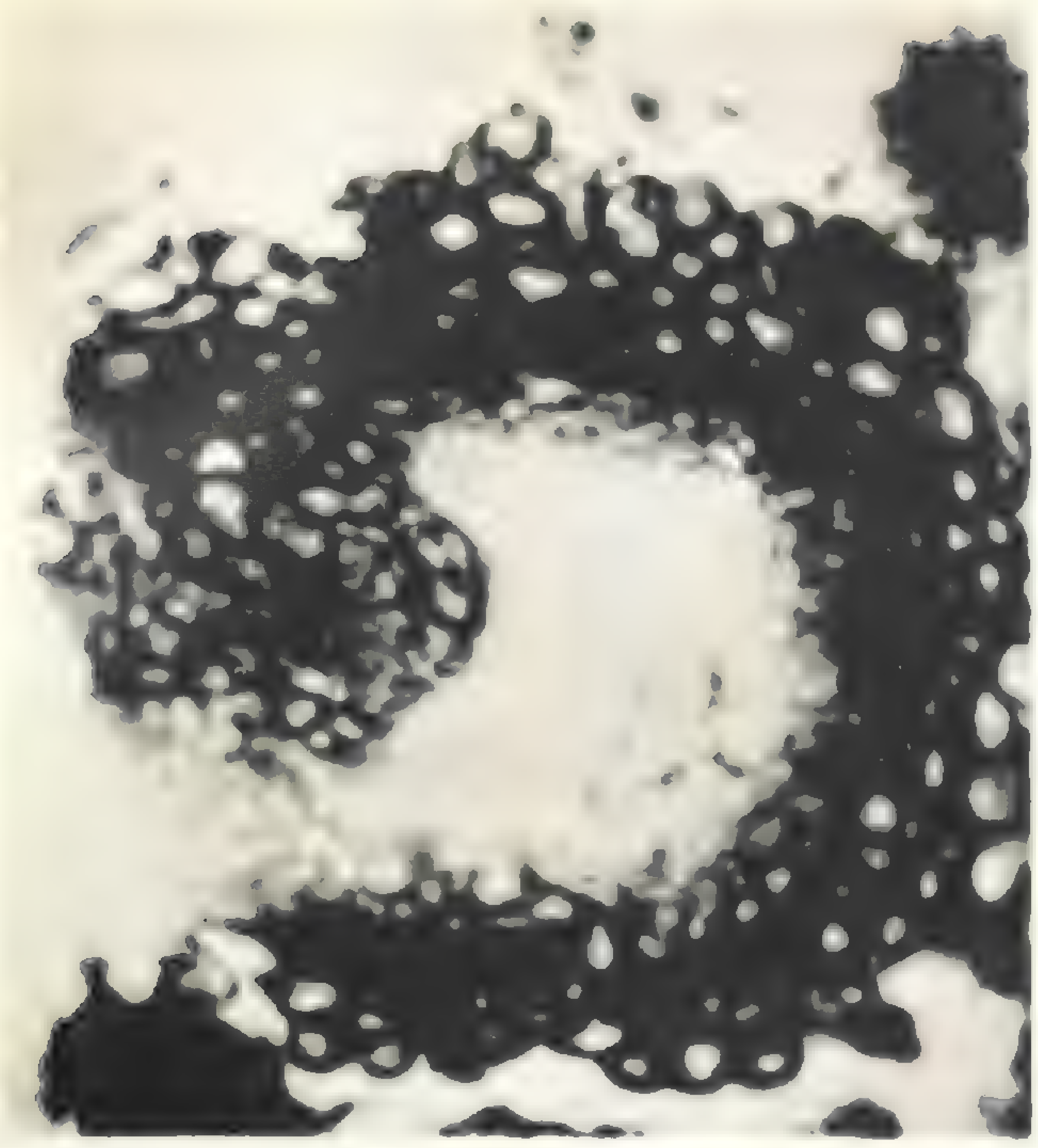
Explanation of Plate

PLATE 13

The microscopic structure of a fertile perithecium.

Figs. 1–3. Serial sections of a fertile perithecium from a Petri-dish culture of B 5 grown on Leonian's agar at 18° C; × 350. In fig. 3, a median section, ascospores are plainly visible.

Fig. 4. The ascospores of fig. 3 shown at a higher magnification; × 865. Note that these spores are 4-septate (3-septate ascospores are usually found in this species).



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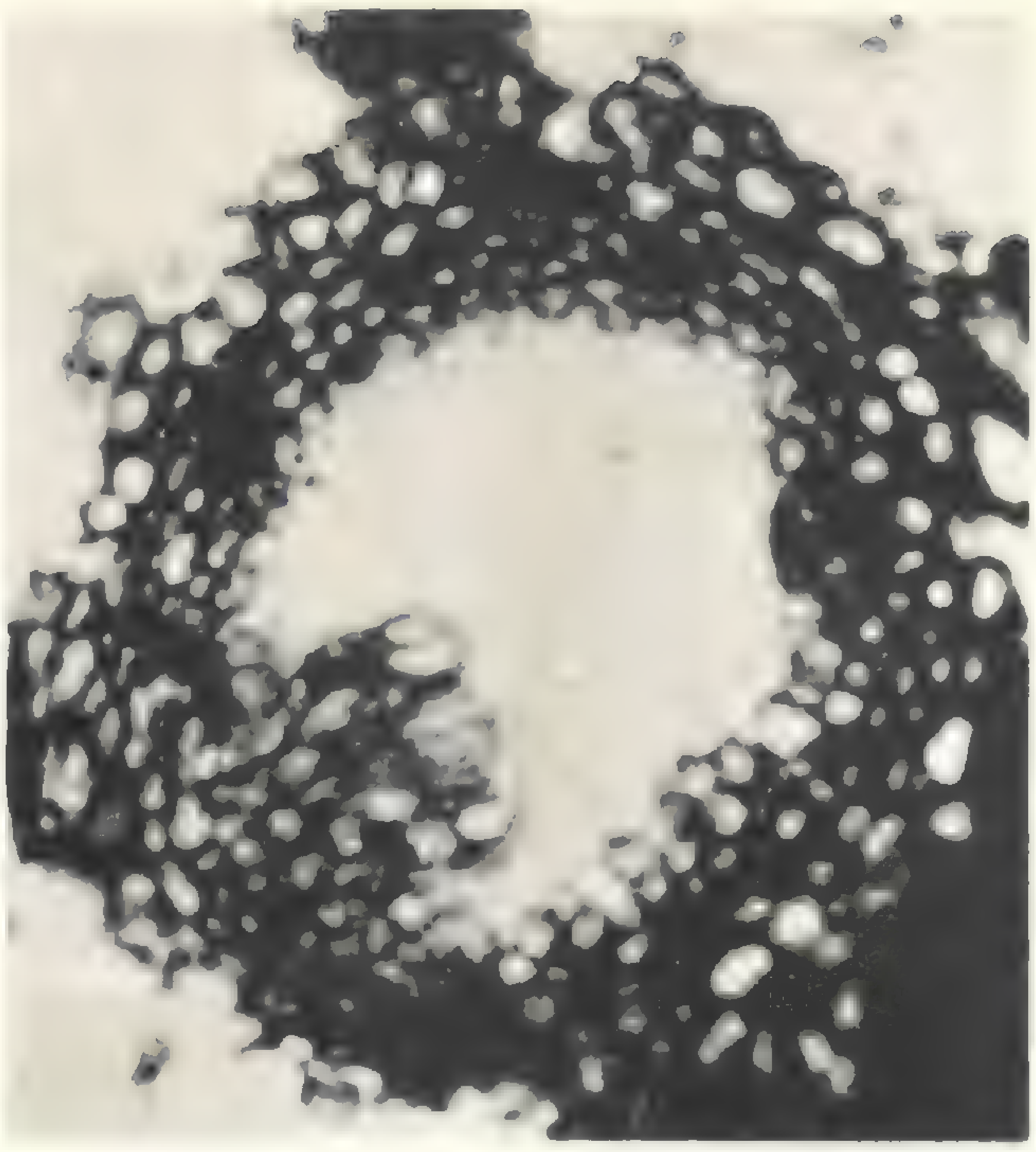

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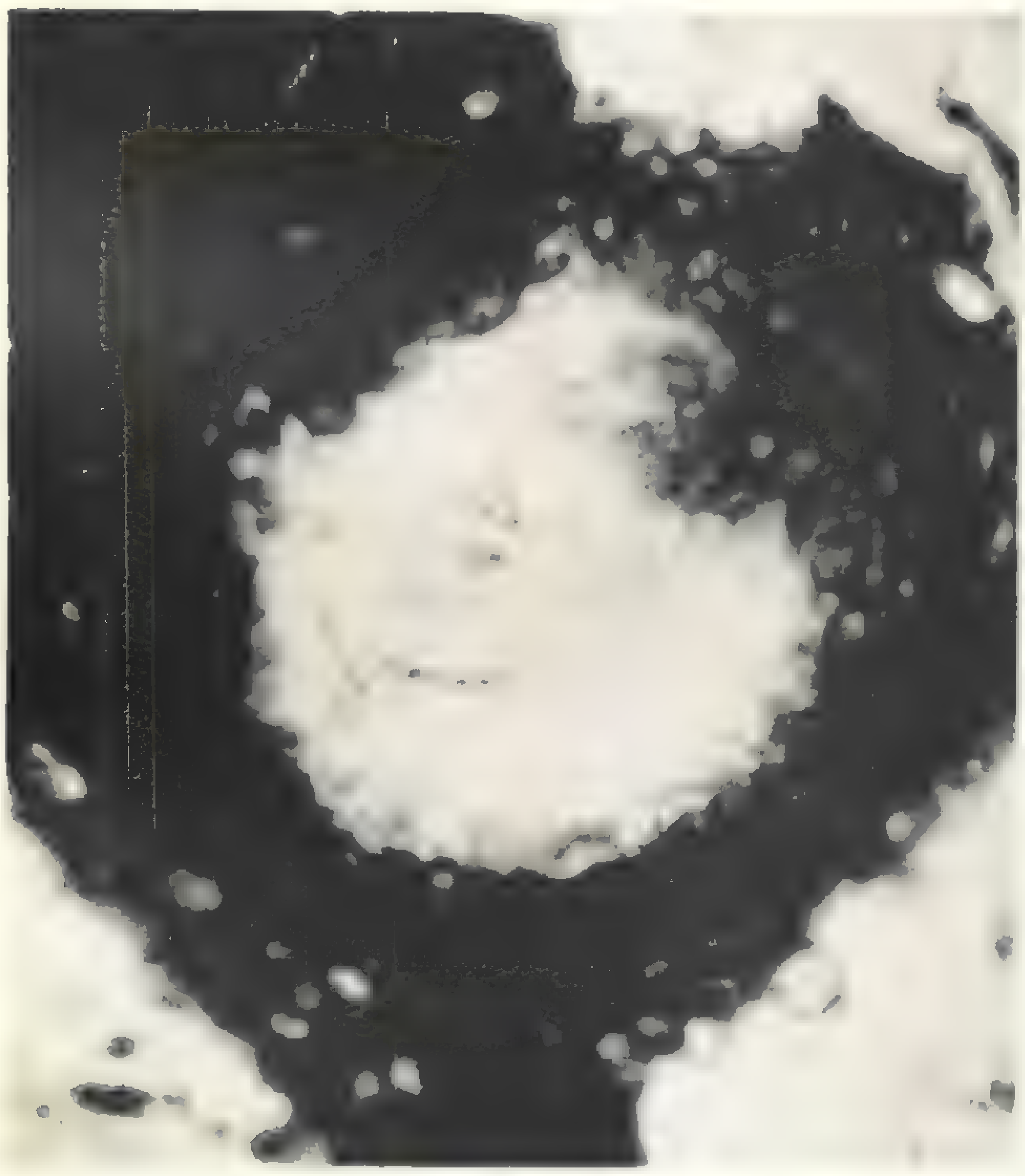

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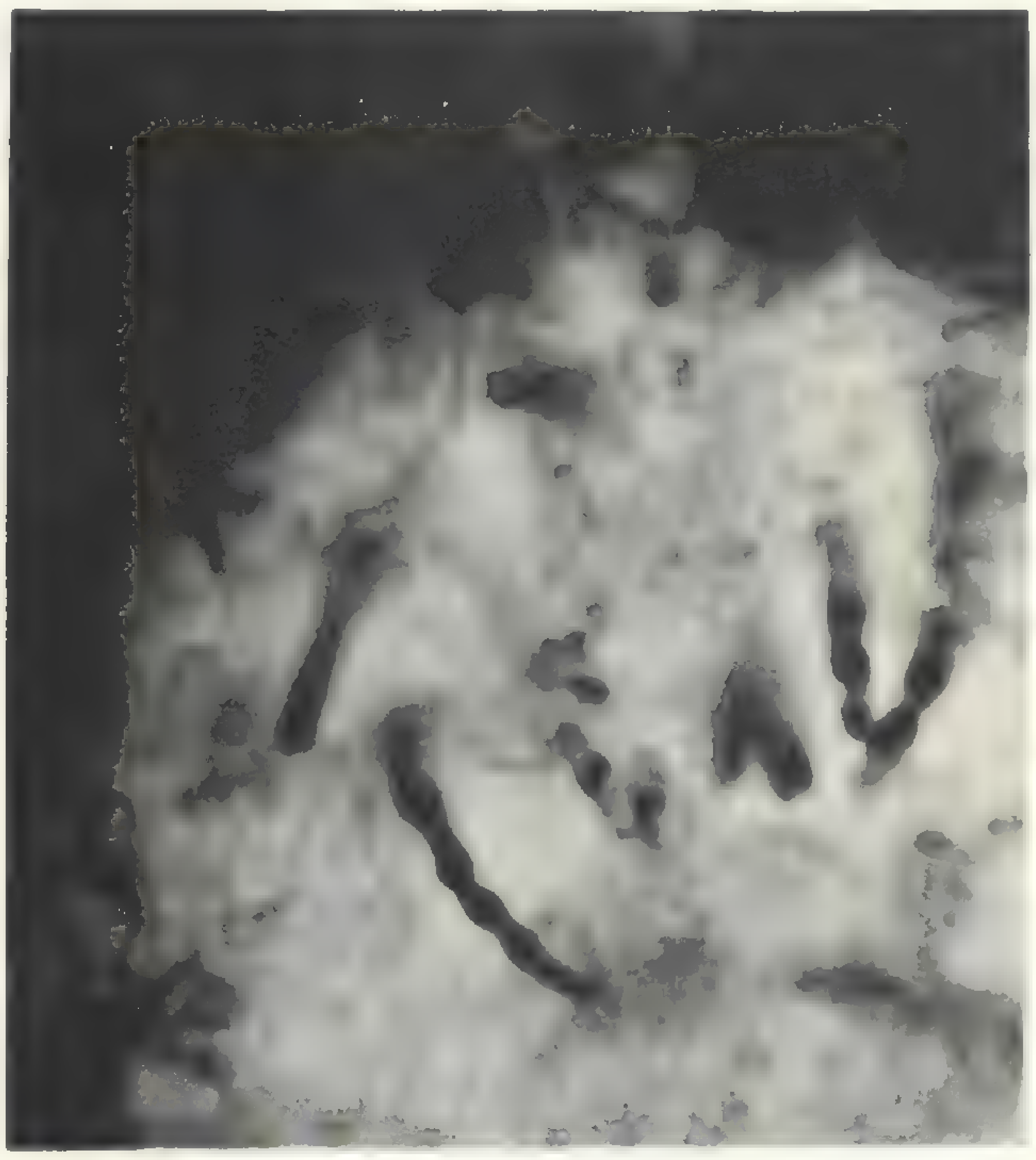

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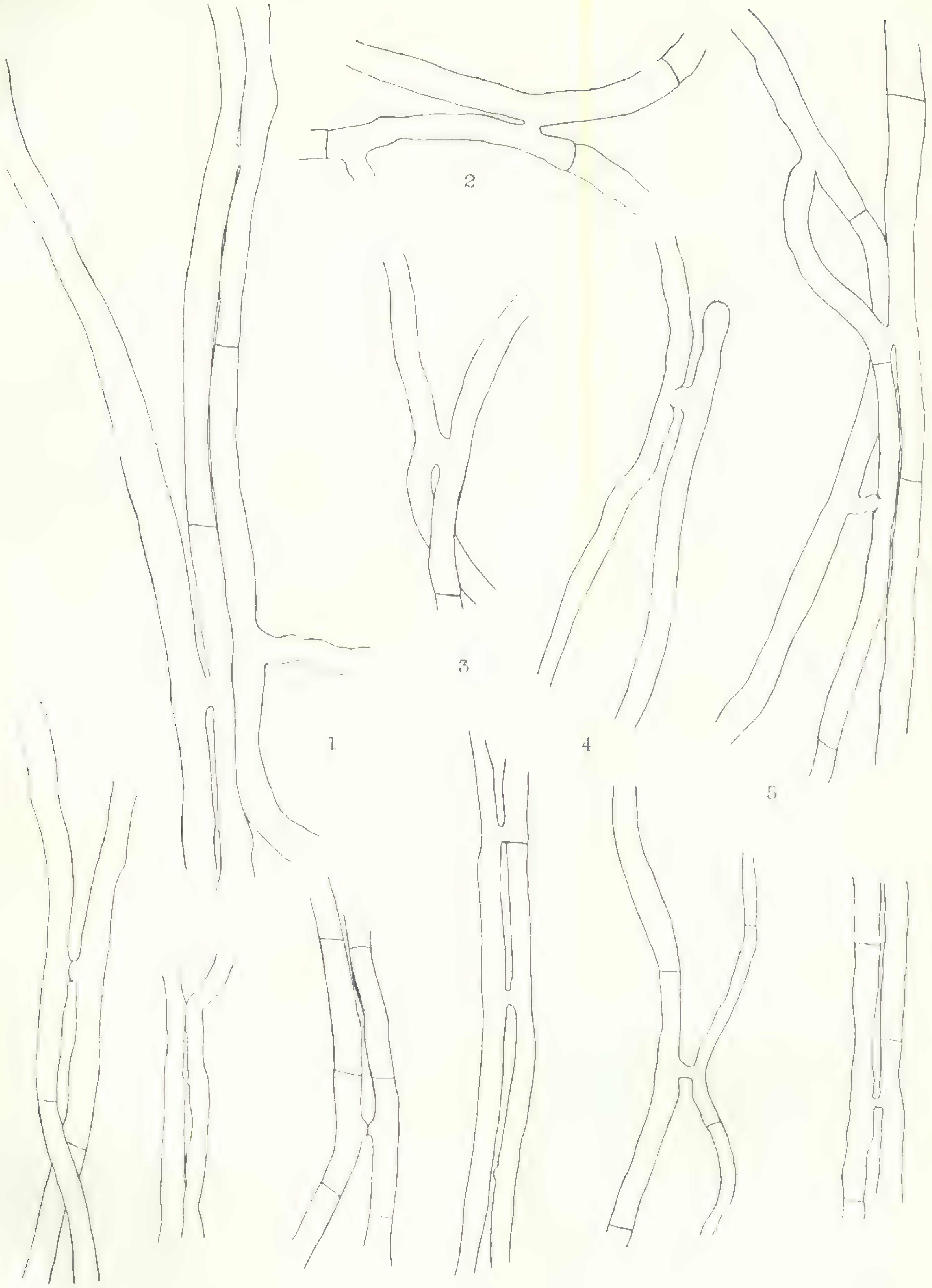
GODDARD—VARIATION IN GIBBERELLA SAUBINETII

Explanation of Plate

PLATE 14

Hyphal anastomoses drawn with the aid of a camera lucida from living material; × 625.

Figs. 1 and 2. B 5–1 × A 35–1.
Figs. 3 and 4. A 35 × A 35–1.
Figs. 5, 6, 7, and 8. B 5 × B 5–1.
Figs. 9 and 10. B 5–1.
Fig. 11. A 35–1.



GODDARD—VARIATION IN GIBBERELLA SAUBINETII

Explanation of Plate

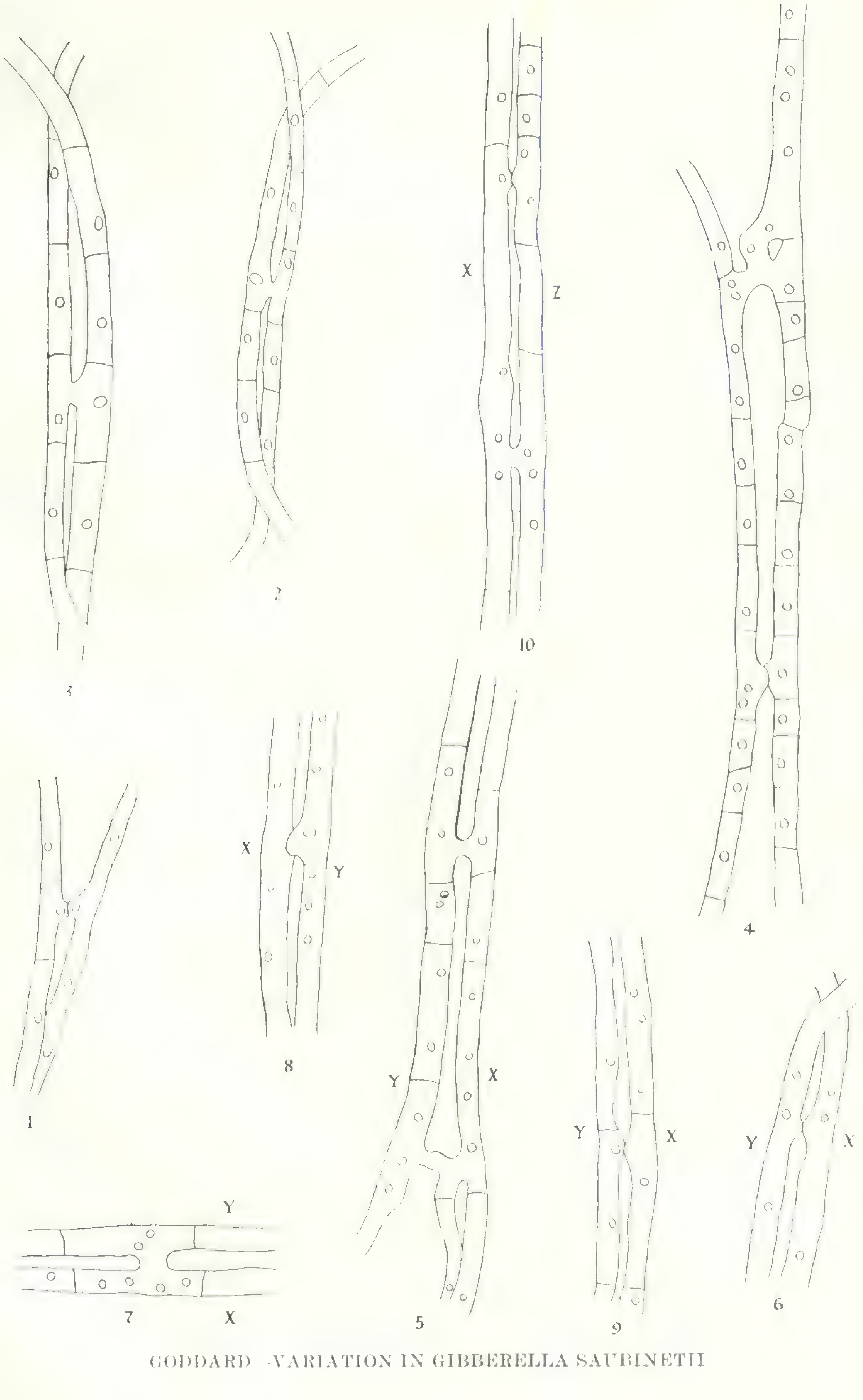
PLATE 15

Hyphal anastomoses drawn with the aid of a camera lucida from stained material; × 450.

Figs. 1, 2, and 3. A 35 × A 35–1; the remainder, B 5 × B 5–1.

Figs. 5–9 inclusive show 6 fusions or beginnings of fusion of hypha X with hypha Y.

Fig. 10 shows hypha X fusing with hypha Z.



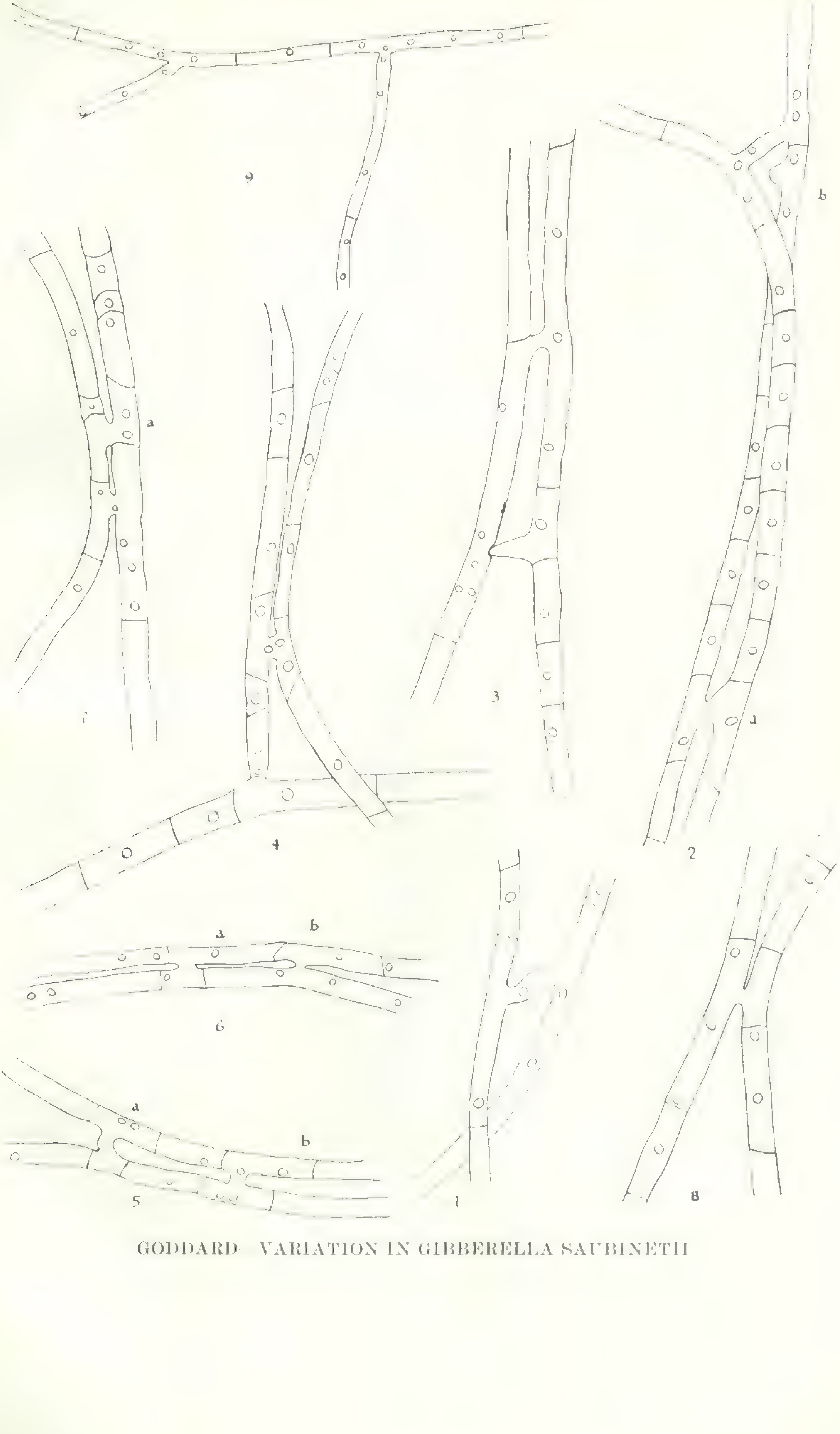
GODDARD—VARIATION IN GIBBERELLA SAUBINETII

Explanation of Plate

PLATE 16

Hyphal anastomoses drawn with the aid of a camera lucida from stained material.

Figs. 1–8. B 5 × B 5–1; × 450.
Fig. 9. A single hypha showing type of branching; × 225.



GODDARD—VARIATION IN GIBBERELLA SAUBINETII

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TREE TEMPERATURES AND THERMOSTASY

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It is commonly assumed that, with minor variations, the temperature of the plant body is essentially that of the surroundings, or to be specific that the root system practically holds the temperature of the soil, while the stem temperature is that of the air. Stiles ('36) states, for example: "Any difference in temperature, however, between the plant and the medium in which it lives is generally very slight, and it has been stated that the temperature of growing shoots is not as a rule more than 0.3° C. above that of the surrounding atmosphere." Pfeffer ('06, Vol. 3, p. 381) says: "Hartig found, for instance, that the interior of a tree trunk sank to –13° C. during a winter when the air was frequently at –15° C. to –22° C. in spite of the upward flow of heat from the warmer roots." Although numerous more or less intermittent records of the temperatures in tree trunks have been made by use of thermometers, it has not been possible, until the invention of modern thermographs, to follow the temperatures, minute by minute, through long periods of time, as in the study to be reported upon here.

Variations of tree temperatures from those of the surrounding air have been noted from time to time. Elevated temperatures were believed to be caused by local, excessive respira-

tion or to slow cooling following periods of high air temperatures due to slow heat conduction of the tissues. Temperatures below those of the air have been assigned to the slow heat conduction of the tissues, or to the transpiration stream pulling cool water from the soil up through the stem. Mason ('25) described a partial thermostatic action in the growth center of the date palm which "is able to neutralize much of either cold or heat as the case may be, that has penetrated from without." This he attributed essentially to "the ascending sap current, with a temperature acquired from the soil from which it is drawn by the roots." Various investigators had previously noted occasions when tree temperatures were either above or below those of the air, but no regulation of tree temperatures except through insulation effects of the bark and the equalization action of soil temperature has been seriously considered. From the results to be reported here it will be evident that under certain environmental conditions there is a distinct thermostatic action in trees involving new concepts of physical conditions within them and resulting in significant benefit to them.

Apparatus and Methods

In planning this study the effort was to attain accuracy together with a minimum of artificial conditions. It was recognized that conduction of heat into and out of the organism by the apparatus might lead to serious error and that intermittent observations might miss important information. After an investigation of several of the chief types of recording instruments, a resistance thermometer was adopted as the most satisfactory. The apparatus, kept in operation for about four years, was an adaptation of a commercial instrument manufactured by the Brown Instrument Company and composed essentially of two main units, the recording instrument (fig. 1) and three sensitive resistance bulbs (fig. 2). The resistance wires of pure electrolytic nickel were enclosed in pyrex glass protective tubes. Although glass has some disadvantages, especially its relatively low rate of temperature conduction, its characteristics seemed less likely to cause error than those

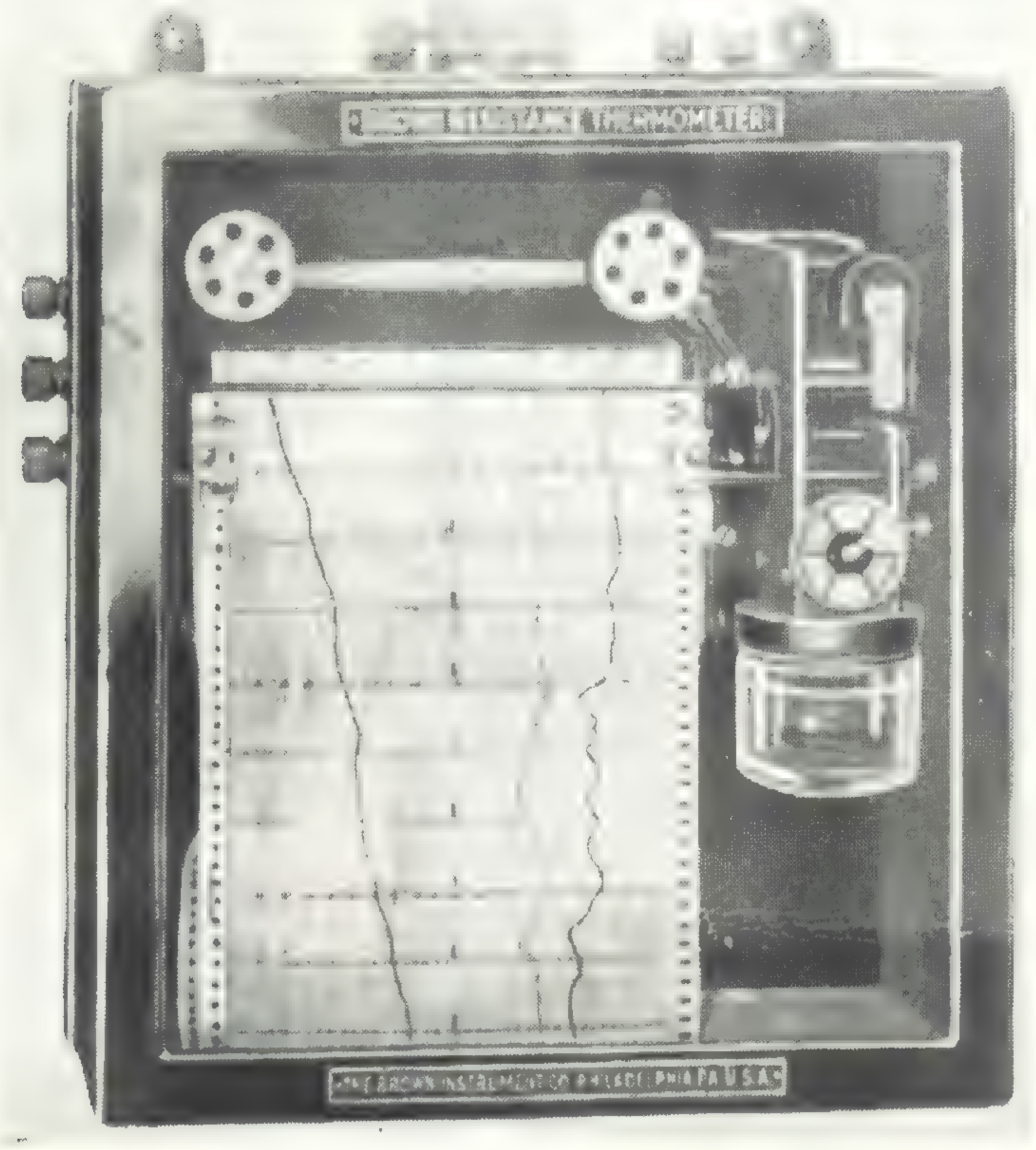

Fig. 1

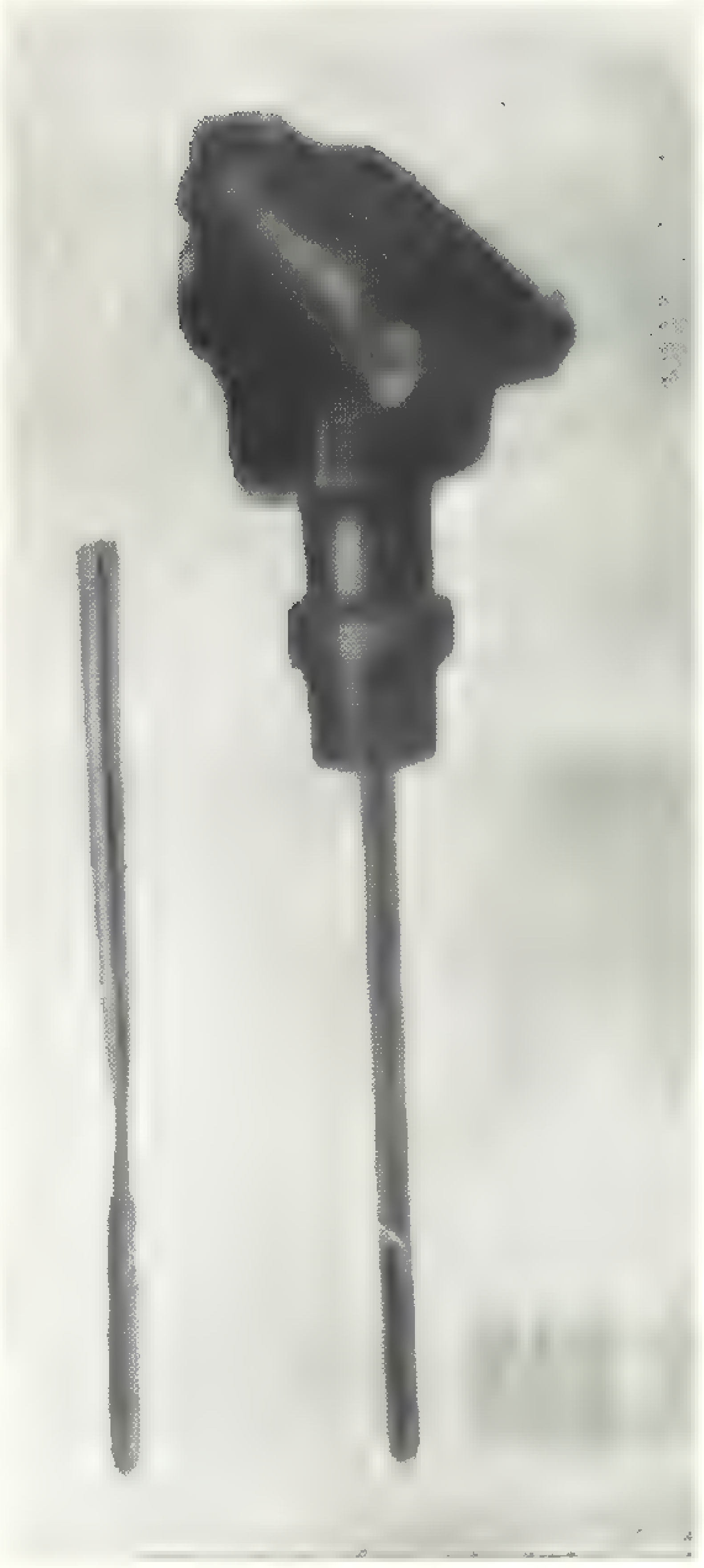

Fig. 2

of other materials. As a means of reducing so far as possible any conduction of heat or cold either from or toward the selected tissue and to give added mechanical protection, a celeron fiber tube encased the glass down to the sensitive elements. A three-wire cable connected each of the bulbs with the automatic recorder.

The recording instrument is described briefly as follows by the manufacturers:

> "It consists of a Wheatstone bridge with two ratio arms of equal resistance, a third arm consisting of a resistor having electrical resistance equal to that of the bulb at maximum temperature, and the fourth arm a resistor having resistance equal to that of the bulb at minimum temperature; a switch permitting transposition of the bulb into the bridge circuit in place of the latter resistor; a galvanometer and storage battery, with standardizing rheostat, being connected to the bridge at the proper points; the galvanometer scale being suitably calibrated in temperature units."

This is a completely automatic, electrically driven apparatus with synchronized clock and a three-record chart in different colors having a temperature range of –35° C. to +40° C. The chart moved at the rate of ¼ inch an hour, and a record of each bulb was made every 3 minutes with a 20-second depression of the needle. Small differences of temperature may most readily be recorded over a range limited only by the recording device; and several different records, covering long periods of time, may be kept simultaneously on the same sheet of paper for direct comparison.

A cottonwood tree (*Populus deltoides* Marsh.), with a trunk about 10 inches in diameter at 30 feet from the ground, where the bulbs were inserted, was selected for study. In setting up the apparatus the three bulbs were distributed as follows: One was inserted with its sensitive element at the center of the tree. The second bulb was placed on the southeast side of the tree, as near the cambium layer as possible, by boring a hole from the opposite side of the trunk. Hence the tissues external to the bulb were left intact, and necessary mechanical support for the bulb was obtained. Both holes were bored to the diameter of the celeron tube to obtain a tight fit. The tight-fitting apparatus was undisturbed for the period of the experiment, so

that its physical continuity with the tissues of the plant was not broken. Much of the success in obtaining the detailed and continuous record described later may be ascribed to this fact. The third bulb, which recorded the air temperature, was placed in a small cage built in imitation of the U. S. Weather Bureau shelters, to screen it from direct sunlight and rain. During the growing season all the bulbs were shaded by the tree foliage.

The immediate problem was to determine accurately the fluctuations of the tree temperatures in relation to those of the air and to discover any indication of a control of the temperature by the tree itself.

It was possible to read readily from the record-charts 0.25-degree changes of temperature and to compare almost minute for minute the temperatures of the three bulbs. Photographic reproductions of many of the original graph-records made during the 4-year study are cited by date in the body of the text and may be identified thereby. The diagram in fig. 3, which is an exact copy of a typical medium temperature record, will help to understand the general principles followed in interpreting the graphs reproduced at the end of the paper.

GENERAL PRINCIPLES FOR READING THE CHARTS

1. The usual record for a 24-hour period shows (fig. 3) the air temperature beginning to rise at from 5 to 8 a. m., reaching a maximum between 1 and 5 p. m., followed by a decline in the late afternoon and night. Commonly the air-temperature line (A) crosses the tree-temperature lines (H and C) during the early morning rise of the air temperature and again in the afternoon with its decline. At these intersection points (W, X, Y, and Z) the air temperature is momentarily the same as that of the tree center (W or Y) or cambium (X or Z). Many modifications of this daily record appear, as will be seen in the graphs, and even complete inversions of the air temperature may occasionally take place when it increases during the night or decreases during the day. Nevertheless, this fundamental type must constantly be borne in mind when these records are being examined.

2. Air-temperature increases, before the morning intersections of the temperature lines, cannot *raise* the tree temperatures because the air temperature is *below* those of the tree.

3. Air-temperature decreases, before the afternoon intersections of the temperature lines, cannot *lower* the tree temperatures because the air temperature is still *above* those of the tree.

Fig. 3. Typical record of the three tree temperatures. The lines A (air), H (tree center) and C (cambium) are the first portions of the temperature records for the 24-hour period, 7 a. m. to 7 a. m. W and X are the a. m. intersections of A with H and C respectively, and Y and Z the corresponding intersections made during the p. m. decline in temperature. Later, W, X, Y and Z are denominated "iso-thermal nodes." In the original graph-records the vertical lines represent 0.5° C. and the horizontal lines, reading from bottom to top, 1-hour intervals from a. m. to p. m. The numbers on the horizontal lines of the graph-records are to be disregarded, but the temperature lines are correctly numbered. In the graph-records and in this figure, therefore, temperature increases from left to right and time advances upward.

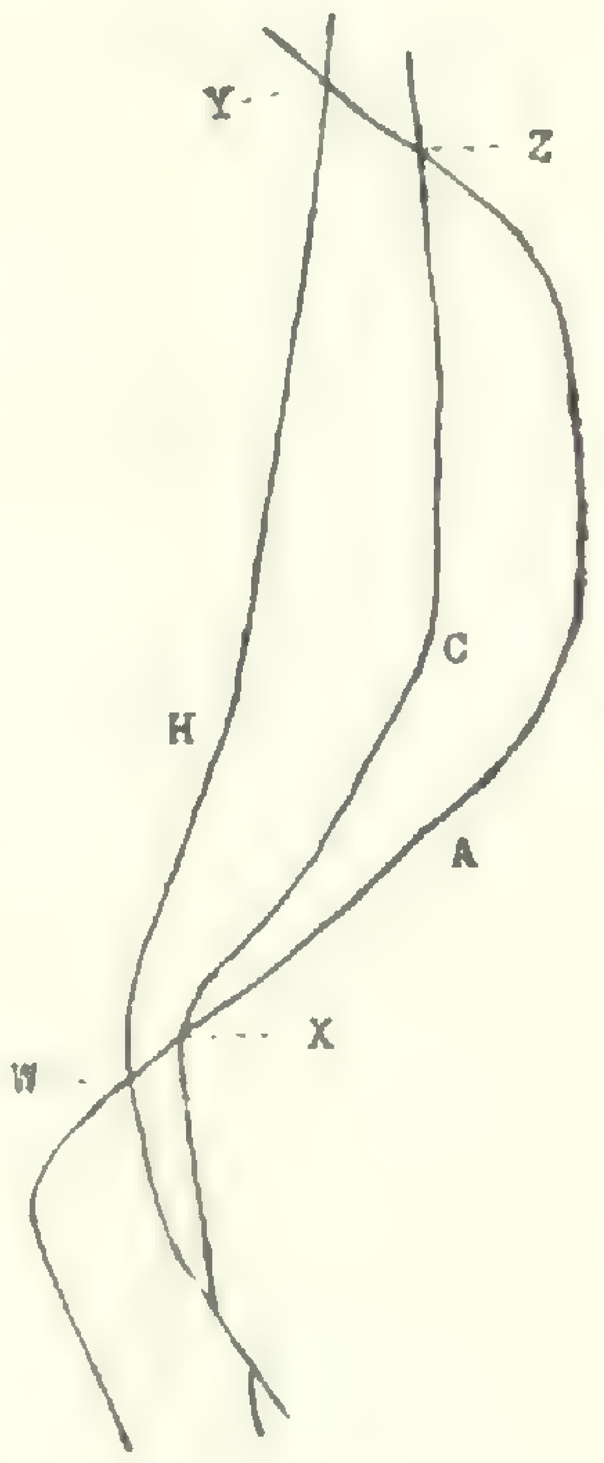

Fig. 3

4. However, such an increase before the intersections W and X in the morning, or a decrease before the intersections Y and Z in the afternoon, does *slow down the rate* of the temperature changes in the tree and hence will prolong the time between the minimum air temperature and the minimum tree temperatures in the morning and between the maximum air temperature and the maximum tree temperatures in the afternoon respectively.

5. From 2 and 3 above, it will be evident that, in calculating the direct effect of air-temperature change upon the tree temperatures, only the number of degrees after the morning intersections and the afternoon intersections respectively should be counted.

6. The same intersections must be used as the basic points in calculating the degree-hours as described later.

7. As long as the cambium temperature is appreciably above that of the center the latter continues to rise regardless of whether the air temperature is rising or falling.

8. Tabulations of maxima and minima or of mean temperatures have not usually been presented, although heretofore most of the published data on tree temperatures have been given in this form. Such tabulations are usually inadequate and often inaccurate due to infrequent or arbitrarily timed observations. Much of the value of the present records would be lost, as has been true of former published data, by the use of mean temperatures, since averages iron out individual differences from which, in studies of this type, principles may be determined. Maxima and minima, as can be seen from numerous examples in these records, very often cover considerable and irregular periods of time and are not merely points, as has usually been tacitly accepted in former studies upon this subject.

"DEGREE-HOURS"

Two methods have been adopted to indicate the quantitative relationship between rise in temperature of the air and that of the tree. Figure 4 is a tracing of the lower portion of a typical graph-record in which LM represents the hour at which the air-temperature line (T_A) makes an intersection in the morning with the tree-center temperature line (T_H) during the daily rise in T_A. The intersection point is A and is referred to as "T_A min." in the discussion and tables. DB represents the hour at which T_A reaches its maximum, and B is "T_A max." E is the point at which T_H begins to rise and is "T_H min." AD is the temperature line on the chart through A. XF is the temperature line on the chart through E. CF equals XE; and FG represents the hour-line through F. G is taken as "T_H max." The reasons for adopting these limitations have been partly indicated in the preceding section, and will be given in detail in further discussions. If the increases in temperatures were perfectly steady and T_A and T_H therefore straight lines, DB and FG would correctly indicate the increases and the ratio

DB/FG would be a measure of the net effect of air-temperature rise upon tree-temperature rise. For certain purposes it has seemed satisfactory to use this ratio as given in some of the following tables. However, since T_A and T_H usually depart considerably from the straight line a more accurate method of estimation was adopted. Any area on the chart, as for example ABD or EFG, bounded by the temperature record line and any given temperature base line and within any given time limits, may be rather accurately determined by counting the small rectangular spaces of the graph paper. The number of these spaces, divided by two, because each space represents 0.5° C., gives the "degree-hours" for this area. The ratio ABD/EFG is taken as a measure of the total net effect of atmospheric temperature change upon the temperature change in the tree over the given period of time.

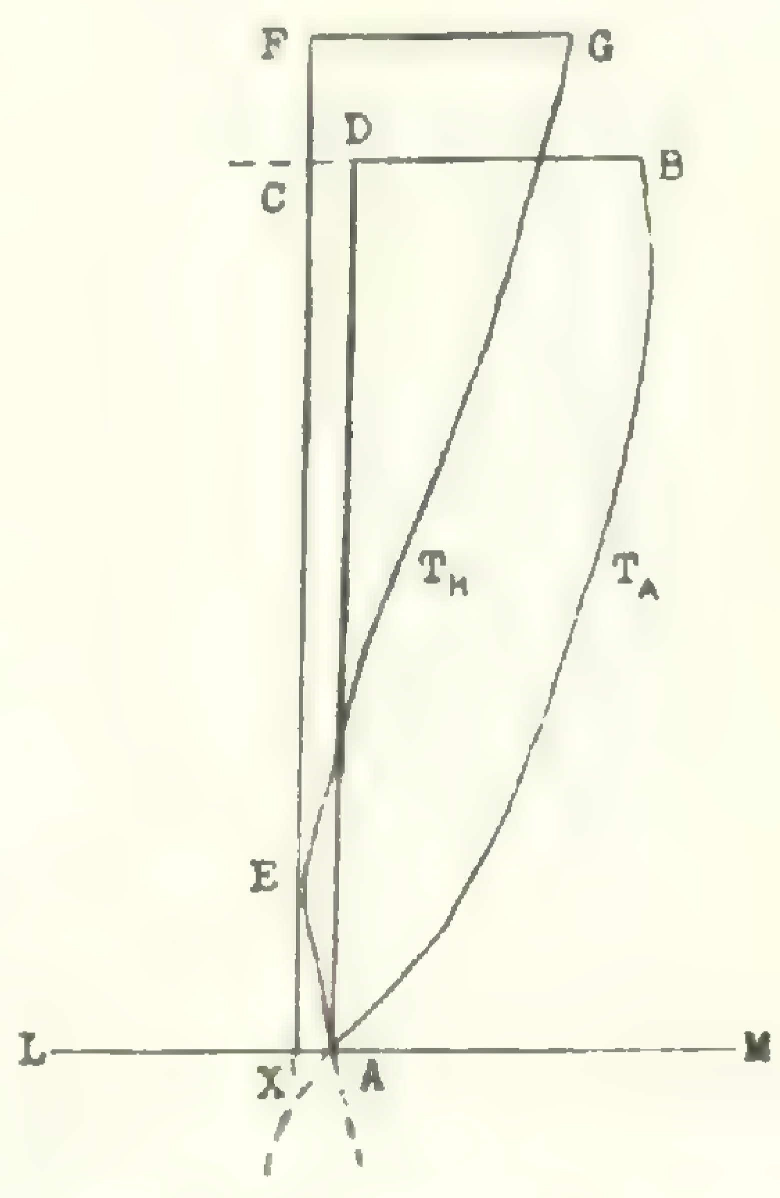

Fig. 4. Method of determining the "degree-hours."

General Results

As would be expected, there is always a "time-lag" between temperatures of the tree and those of the air. This occurs in a temperature change, as well as in the attaining of a maximum or of a minimum, and is greatest at the center of the tree. The length of this "lag" period is extremely variable, depending upon the interrelations of a number of factors. Since the physical conditions in the tree and the environmental factors are so variable, the results of the investigation are best considered under three headings: (1) "low" temperatures, from about 10° C. downward; (2) "high" temperatures, from about 30° C. upward; and (3) "medium" temperatures, in the intermediate zone. The limits of these three temperatures ranges are only very broadly placed, and under certain conditions the "medium" range extends above or below the limits indicated. The

generalizations stated below are supported by selected "case studies" given in detail later.

LOW TEMPERATURES

One of the outstanding tendencies during the colder portions of the year was for the tree temperatures to remain steadily at 0 to –1.5° C. for many hours while the air temperatures might be steadily dropping below freezing or rising above that point. Fluctuations between day and night air temperatures were often not reflected at all or only slightly in the tree temperatures, whereas a corresponding number of degrees of change at moderate temperatures directly affected the tree temperatures. Thus there was exhibited a buffer action which tended to prevent frequent changes in temperature across the freezing point. On the other hand, after 24–48 hours or more, if the air temperature continued to change in the same direction, the tree temperatures began to follow the general course of the air temperature and eventually approximated any steadily maintained air temperature.

HIGH TEMPERATURES

During the summer of 1934, and especially the latter half of the month of July, high temperatures and low atmospheric humidities provided an exceptional opportunity to study the relationships of tree temperatures to high air temperatures in the absence of many of the usually complicating factors.

When the air temperature rose to above 35° C. and there was a low relative humidity, the center temperature of the tree dropped contemporaneously over a variable period of time until an equilibrium was reached, after which it began to rise with the drop in the air temperature. On the hottest days, when the air temperature was 42.5° C., the center temperature was 27 to 27.5° cooler. On other days the center was 22 to 26° cooler than the air with a low varying from 15 to 17° C. If, during the day, the air temperature rose and fell more than once, the center temperature of the tree changed in the opposite directions immediately. The rate and amount of change were less than

those of the air but were in a definite ratio to the air changes. Frequently during July 18–25 a sudden rise or fall of even 1.5° in the air temperature produced an immediate drop or rise respectively in the center temperature of 0.5° or more. The cambium temperature varied much less sharply than that of the center and air. It tended to rise in the morning with that of the air, but later attained an equilibrium between the air and the colder center temperatures. A subsequent slow rise, usually culminating about 5 hours after the beginning of the drop in the air temperature, varied slightly with the speed of change in the center and air temperatures. Thus, on July 19, 1934, at 4 p. m. when the air temperature (39.5° C.) began to drop, the center temperature was 17° C. while at 7 a. m. the next day it was 22° C. Here was a rise of 5° in 15 hours in the tree center occurring simultaneously with a drop in the air temperature of 13°. The cambium meantime had changed only from 30.5 to 32.0° C. On July 20, from 5:30 p. m. to 2 a. m. the center temperature changed from 16.5 to 21° C. and the cambium rose from 31.5° to only 32.5° C. in 5.5 hours. The cambium temperature usually rose with the rise of the center temperature and against the drop in the air temperature, although concurrent with a rapid rise in air temperature there was at times a temperature increase in the cambium.

From these observations it is clear that the temperature of the cambium region is a resultant of the cooling effect of the tree temperature acting against the absorption of heat from without. During the early morning of July 14 the rapid drop in the air temperature carried it below the two tree temperatures. During the same period the influence of the temperature of the air on that of the cambium is shown by the decline of the latter. As the temperature of the air began to climb, however, and that of the center began its daily drop, the cambium temperature tended at first to follow the direction of the air but finally took the downward course of the center temperature. The effectiveness of this thermostatic action is seen in the records, for example, of July 21 and 22. Early in the morning the cambium temperature began to rise with, and to follow fairly

closely, the air temperature until the cooling effect of the center definitely pulled it down again in about three hours, even when the air temperature was still rapidly rising. At other seasons of the year the cambium was often at the same temperature as that of the air.

It appears that there is only one adequate cause of the almost instantaneous reduction of temperature of the center of the tree during the periods of high temperature increases. High air temperatures, both directly and through effecting a rapid decrease in relative humidity, set up an increased transpiration which caused a certain water deficit in the tissues of the tree. This in turn resulted in a rapid interior vaporization of water which absorbed large amounts of heat, thus cooling the tissues.

MEDIUM TEMPERATURES

At moderate, steady temperatures, associated with other steady climatic conditions, the two temperatures of the tree, which ran close to those of the air, were almost identical, and their rise usually began very soon after that of the air. However, the beginning of the decline in the cambial temperature was usually delayed 3–4 hours after the initiation of the fall in the air temperature, while that of the tree center was frequently delayed 1 to 2 hours longer, during which time the latter even continued to rise. When there were gradual changes in the air temperature the changes in tree temperature kept pace, with only slight lag. When there was a more rapid and sharper change in the air temperature, as frequently in passing from night to day, the tree temperatures showed much less change. Thus differences between day and night air temperatures of about 16° were reflected in corresponding tree temperatures by differences of only 2.5 to 3.5° (table 1).

At times, even under moderate conditions, as on July 15, 1932, increases in air temperatures resulted in slight, but definite, slow reduction in the center temperature, thus exhibiting the thermostatic tendency; and at other times the cooling action is evidenced by an unusual wide spread between the air-

TABLE I

Date 1934	Air temp.	Time	Cambium temp.	Time	Center temp.	Time
May 27–28	High 27 Low 11	12 m. 4–5 a. m.	20.5 17.0	8 p. m. 7 a. m.	19.5 16.5	9 p. m. 8–9 a. m.
	Diff. 16		3.5		3.0	
28–29	High 29.5 Low 13.0	12 m.–4 p. m. 5 a. m.	22.0 18.5	8–10 p. m. 7 a. m.	20.5 18.0	10–12 p. m. 8 a. m.
	Diff. 16.5		3.5		2.5	

and the tree-temperature lines. However, at moderate temperatures this tendency was often obscured by other factors.

When the air temperature was between 20 and 30° C. the cambial temperature kept close to it. During periods of slight, slow changes of air temperatures, cambial temperatures were often maintained 0.5 to 1.5° above those of the tree center, regardless of whether the air temperature was above or below that of the tree center. This might seem to indicate a tendency for the cambium region to maintain its own temperature somewhat independent of the influence of the air and center temperatures.

We may conclude that, at or near the critical temperatures of freezing and of heat injury to protoplasm, living cells of the tree trunk are partially protected through special physical adjustments. These physical adjustments, during high temperature periods, are dependent upon the excessive transpiration often induced by heat. Hence during such periods not associated with excessive transpiration the tree might not exhibit the physical adjustments indicated above; and under high transpirational conditions, induced by other factors than excessive temperatures, an increased internal vaporization might be induced.

Detailed Study of Specific Periods

LOW TEMPERATURES

The temperature of the cambium layer is mainly influenced by that of the air, but it is evident that in the changing climatic

conditions of the area in which these studies were made the cambium layer and the air are seldom at the same temperature. When the temperature of the air is on the decline that of the tree center is usually higher than that of the air, while with the air temperature rising the tree center is soon colder than the air. This relatively warm or cold center slows down the upward and the downward tendencies of the cambium temperature in response to the rise and fall of the air temperature respectively. This was particularly evident when the air temperature line crossed the zero temperature line in continuous upward or downward swings following a steady period below or above zero. After an adjustment in the tree had been made at about the zero line the temperatures followed the direction of the air temperature with relatively slight lag in time but did not usually reach the extremes of the air temperature until the latter had become steady for several hours. These conditions, as well as the usual buffering action at the freezing point, are well illustrated by the following typical examples.

1. The tendency for the temperatures of the tree to follow closely those of the air after the tree had become adjusted to freezing weather is shown by the cold spell in the early part of March, 1932. From March 8 to 12, the tree temperatures closely paralleled those of the air which varied most of the time from –3.0 to –10.0° C. Also, during the night of March 12–13, 1932, the air temperature dropped from –3.5° to –9.5° C., and in an essentially coincidental drop the tree-center temperature reached –8.5° C. an hour later. This period had been preceded by 36 hours of sub-freezing temperatures in the tree, the cambium having attained a minimum of –4.0° C. and the center –4.75° C.

The following specific examples illustrate well the usual buffering action at the zero line, by which the tree temperatures are held steadily at or close to zero for many hours or by which the cooling of the tree tissues is considerably slowed down.

2. At 11:00 p. m., November 14, 1932, the air temperature dropped from 14.0 to 9.0° C. in 0.5 hour, followed by a slower almost uniform drop to –8.0° C. at 6:30 a. m., November 16, or

a total drop of 22.0° in about 32 hours. The cambium and center lines began their drops in 0.5 and 1.5 hours respectively, and after 2.5 hours they were essentially superimposed. The center temperature reached zero at about 10:00 p. m., November 15, 23 hours after the beginning of the cold spell and 11 hours after the air temperature crossed the zero line. It then very slowly dropped in 8 hours, November 15–16, approximately 1.0° more, while the air temperature dropped from –5.0 to –8.0° C., giving a ratio of air temperature drop to tree temperature drop of 3:1. During the night of November 17 and 18 the air temperature dropped from –0.25 to –6.0° C. in 10 hours, while the tree center dropped only from 0.25 to 0.50° C. in that time. This gives a ratio of 23:1. On November 19 a 4.0° air-temperature drop resulted in a 0.5° drop in the tree center, or a ratio of 8:1. From 9:00 p. m., November 15, for more than 6.5 days, the cambium temperature was about a degree higher than that of the center, while neither showed more than a slight variation up or down. Meantime, the air temperature was mainly somewhat below zero, but with short, upward turns to about +5.0° C. on November 17 and 18, and 16.0° on November 20. Finally, on November 22, following a 12-hour rise in air temperature to about 8.0–10.0° C., the cambium, at 3:00 p. m., and the center, at 10:00 p. m., began their periods of rise. This case history demonstrates the tendency for the tree temperatures to remain at about zero even when the air temperature alternated from –8.0 to +16.0° C. It also shows, under an essentially constant zero tree temperature, the tendency for the temperature of the cambium to remain slightly higher than that of the center, even when that of the air is mainly below both tree temperatures.

3. At about 4:30 p. m., December 6, 1932, a sharp drop in air temperature from about 20.0 to 5.0° C., followed by a slower decline to a minimum of –10.00° C., initiated an 11-day period of sub-zero weather, mostly between –5.00° and –10.00° C. During the first 28 hours after the center temperature reached zero the cambium remained about 0.5° above the center temperature, with the cambium attaining and holding a temperature of

–0.5° C. Then the cambium line gradually crossed the center line at about –1.25° C., and for more than 24 hours the cambium temperature remained about 0.5° lower than the center, while both temperatures were dropping to approximately –5.0° C. This case illustrates the usual tendency, under these conditions, for the cambium to hold a temperature during day and night slightly higher than that of the center while both remained at about zero. It shows also the tendency for the cambium subsequently to respond somewhat more rapidly than the center, as it does at more moderate temperatures, to the further changes in the air temperature. During the long cold spell following the above initial drop in temperature the air temperature, on December 7 and 8, fell from –5.0° to –9.75° C., while the tree center fell from 0.0° to –1.25° C., a ratio of 3.8 :1. During the next two days a drop in air temperature from –3.5 to –10.00° C. brought about a drop in the tree center from –1.0 to –1.75° C., a ratio of 8.6 :1, while from December 9 to 10 an air-temperature drop from –7.5 to –9.5° C. caused a tree-center drop from –3.0 to –5.00° C., a ratio of 1 :1. This shows that after the tree had been at a sub-freezing temperature for an extended period, in this case approximately 45 hours, a degree of air-temperature reduction was much more effective in lowering the tree temperature than when the tree had been only for a short time at the sub-zero temperature. This greater effectiveness of a change after a long period of sub-zero air temperatures is shown in a further drop in temperature beginning about 7 p. m., on December 11, 1932. In 12 hours the air temperature dropped from –2.75° to –15.50° C. Correspondingly the tree center dropped from –3.75° to –11.25° C., a total of 7.50°, giving a ratio of 1.7 :1.0. The tree tissues had constantly been at sub-zero temperatures from the morning of December 8.

4. From December 19 to 22, 1932, the tree center held steadily at –0.5° to –1.5° C., with the cambium usually about 1 degree higher, although at one time the air temperature was above zero for more than 24 hours with a maximum at 11.5° C. Finally, on December 22 to 23, a rise in air temperature to +14.0° C. caused a slow rise in the tree temperatures almost to

that of the air, with the cambium temperature at the time of the air maximum 1 or 2° higher than that of the center. On the downward swings of the curves between December 7 and 22 the cambium- and center-temperature lines soon (3–4 hrs.) became superimposed, when the air temperature change was 5–8° C. in 12 hours; or the cambium assumed a temperature slightly below that of the center when more rapid or extensive depressions of the air temperature occurred.

5. From about 3:30 p. m., March 9, 1934, for 60 hours there was a zero to sub-zero air temperature reaching –12.0° C. in a continuous drop from zero in 14 hours. Twice it rose to +1.5° C. for an hour or less, but otherwise it was mostly zero to –4.5° C. During all of this period the center tree temperatures were from –1.50° to –1.75° C., and the cambium about –0.5° C., except at the coldest period when it was –1.0° C. For the total period the ratio of T_A drop to T_H drop was 4.7:1.

6. The period of 34 hours, from March 18 to 19, 1934, with an air temperature minimum of –10.25° C., gave rise to a steady tree-center temperature of –0.5 to –2.0° C. for about 35 hours, beginning about 8 p. m., on March 18. During the initial change T_A dropped from 16.0° to –4.5° C., while T_H dropped from 16.5° to 1.0°, or a ratio of 1.3:1. During the second significant lowering of temperature T_A dropped from –1.0 to –9.5° C., while T_H dropped from 0.25° to –2.0° C., or a ratio of 3.7:1. In this case, approximately three times as many degrees of change in air temperature were necessary to cause one degree change in the tree temperature at or immediatly below zero as above it.

7. On March 5, 1932, at 3:30 a. m., there was a sharp drop in air temperature from 5.50 to –11.25° C., in about 28 hours. The tree-center temperature began to drop about 1.5 hours later, and the cambium in 0.5 hour. Thus there was a "lag" of only 1.5 hours in the beginning of the response of the center temperature to the change in air temperature. At this season of the year there is little or no heat used in the vaporization of water in the tissues, and at this time of day no direct insolation to complicate the situation. At temperatures above 0.0° C. the complications of freezing action are also absent. This is ap-

parently a good example of "lag," due simply to the rate of heat transfer through the tissues. For over 56 hours the air temperature remained at –4.0 to –11.5° C., and for about 28 hours from the time that the tree temperatures reached 0.0° C. they held between that point and –1.25° C. For about 10 hours after the tree temperatures had reached zero they declined further only when the air temperature decreased again. For example, when the air temperature remained at –7.00 to –7.25° C. for 6.5 hours (7:30 p. m. to 2:00 a. m.), the tree center remained at –1.0° about 8 hours. Following the further drop in air temperature, the tree temperature began to drop slightly, and minor fluctuations continued in accord with those of the air. There was then a period of several hours of adjustment, near the zero line. Later, when the air temperature remained steadily at –11.0° C. and even after it began to rise, the tree temperature continued to fall for at least 6 hours. In this period the tree-temperature reaction was similar to that under moderate temperatures. During the first decline in air temperature the tree center dropped 6.25°, while the air temperature made its drop of 16.75°. This gave a ratio of T_A to T_H of 2.6:1. During the second period of decline the ratio for the last 12 hours was about 1.3:1, which indicates that the zero-line adjustment had almost been completed in the preceding 32 hours.

8. On January 29, 1932, a sub-freezing period of 3 days with minima at –11.5 and –9.0° C. began. A steady drop in air temperature from 5.0 to –11.5° C. carried the tree center from 9.5 to 1.0° C. The ratio for this period above zero in the tree was 1.05:1. While the tree temperature was crossing the zero line from 1.0 to –1.50° C. the air temperature dropped from –4.0 to –11.5° C., which gave a ratio of T_A change to T_H change of 3:1. During this time the tree temperatures remained steadily at 0.0 to –2.0° C. and continued so 24 hours longer in spite of almost continuous air temperature of 5.0° C. during this latter period. The cambium temperature then began a slow rise to a maximum of 2.5° C., with an air maximum of 9.5° C. Meanwhile the center temperature remained steadily at –1.0° C. for another 4 days despite air temperatures for several hours from 5.0 to 13.0° C. on the last of these days.

9. The tendency for the tree temperatures to hold at or near 0.0° C. during frequent and sometimes rather extensive upward and downward changes of air temperature is further shown in the record of November and December, 1932. For example, from November 16 to 22 the tree temperature was essentially unchanged, while the air temperature shifted from –7.0° C. at night to +10.0° and once to +16.0° C. in the daytime. During this period the cambium temperature continued almost uniformly at +0.5° C., and the center at about –0.5° C.

10. From noon, January 12 to midnight, January 13, 1931, the center temperature remained at 0.0 to –0.5° C., and then slowly fell to –3.0° C. at noon the next day. It rose again in 12 hours to –1.0° C., and then for 3.5 days remained at –1.0 to 0.0° C. in spite of continuous air temperatures of 13.0 to 6.0° C. In this and two succeeding cases there is especially demonstrated the slow reaction of the tree temperatures at the zero line when the air temperature passes above zero after having been for some time below the freezing point.

11. Following the sub-zero period ending February 28, 1934, the air temperature rose and remained above zero almost all of the time for 80 hours, for 68 hours varying from about +3.5 to +10.0° C. During the entire period the center temperature held steadily at –1.5 to –0.5° C. and finally zero. The cambium stood at zero for 44 hours, with a gradual rise above that point for the rest of the time.

12. That the tree resisted temperature change when it had been at a steady sub-freezing temperature was shown on March 12, 1934. An air-temperature rise to 18.0° C. gave a total of 90 "degree-hours," while only in the latter part of this period the tree center had a 3 "degree-hour" rise, or a ratio of 30:1. This contrasts sharply with the degree-hour ratios for periods of moderate temperatures as shown elsewhere.

13. About 9 a. m., January 28, 1934, the air temperature dropped steadily from about 10.0 to –16.5° C., a total of 26.5° in about 24 hours. When the air temperature was –14.0° C., the superimposed tree temperature lines were carried across the zero line without any apparent retardation in rate of fall. Following a rise of a few degrees there was a second period of de-

cline in temperature, during which that of the air was 7.75° C., and of the tree center 5.0° C. This shows a ratio of 1.55 :1. During the first period of decline the tree center dropped 12.0° in response to the 26.5° of the air, or a ratio of 2.2 :1. Hence, although no visual retardation occurred at the zero line it is evident that during the first period a 2.2° change in air temperature was necessary to cause a 1° change in the tree, while during the entire second period after the internal adjustments had been made, only 1.55° of change in the air temperature was needed to cause 1° change in the tree temperature. This latter value agrees very well with the cases cited for periods of temperature change after the zero line adjustments had mainly been made. During the second period a change in speed of drop in the tree temperature occurred at about 10 p. m., January 29, although no change in speed for the air-temperature drop is evident. From that point to the end of the period the ratio between the two temperature declines was 1 :1. Since this occurred during the night when there were no complicating conditions, it demonstrates that the theoretical value for this relationship may be actually reached when there are no restraining influences. The attainment of this value also emphasized clearly the retarding influence of the zero line on the decline in tree temperatures, during the first period, when the ratio was 2.2 :1.

HIGH TEMPERATURES

The marked, thermostatic response of tree temperatures to changes in air temperature during periods of extreme heat was first noted in the records for the latter portion of July, 1934, although records of other years give the same indications in a less extreme form. The graph-records for the period of July 15 to 26 reveal the principal fact that with every morning advance in air temperature there was usually an immediate decrease in the tree temperatures and with each afternoon decrease in air temperature there was a corresponding immediate increase in the tree temperatures. For the whole period, table III lists the data which show that for 2.48° rise in air temperature there was a 1.00° lowering of the temperature of

the tree center and for each 2.83° drop in the air temperature there was a 1.00° rise in the tree-center temperature. It should be noted that, in view of the cause of this phenomenon as indicated later, these ratios represent maximum values, since a more complete insulation would have more successfully prevented heat interchange with the environment, and it would have taken a smaller change in air temperature to effect a degree change in the tree temperature. Also it should be noted, as indicated in table II, that throughout this period the tree temperatures averaged much below those of the air, and that, in contrast to periods of moderate temperatures they were seldom *directly* influenced by fluctuations in the external temperature.

TABLE II

MAXIMUM EXTREMES

1934 July	Tree center T_H min.	Diff. T_A max. and T_H min.	Air T_A max.	Diff. T_A max. and T_C min.	Cambium T_C min.
20	16.5° C.	26.0°	42.5° C.	11.0°	31.5 to 32.5° C.
21	16.5° C.	23.5°	40.0° C.	9.0°	31.0 to 32.0° C.
22	16.0° C.	23.5°	39.5° C.	8.5°	31.0 to 32.0° C.
23	15.0° C.	27.5°	42.5° C.	11.0°	31.5 to 32.5° C.
24	15.0° C.	27.5°	42.5° C.	10.5°	32.0 to 33.0° C.
25	15.5° C.	27.0°	42.5° C.	10.5°	32.0 to 32.5° C.

During the day throughout this period the line registering the cambium temperatures was always between the other two lines and usually about 10° below that of the air temperature. This shows that some influence antagonistic to the heating action of the atmospheric temperature was at work. The chart indicates clearly that the cold central zone provided this influence. Radiation of heat from the cambium zone inward kept this zone from attaining the temperature of the ambient air and its temperature therefore was a resultant of the heat from without and the cold from within. Had this tissue been located midway between the center and the outside it would be expected that its temperature would have approximated the average of the air and center temperatures. However, when, as on July

15, 18, and 20–25, the maximum air temperature of 38–42° C. continued for from 4 to 6 hours the cambium-layer temperature would be expected to rise rapidly due to continued absorption of heat from the outside. Nevertheless, during this period, because of the counter cooling action of the central cold zone, it usually remained almost constant, or with only a slight increase. During certain other portions of the year in such a period of uniform air temperature when the various other factors were steady the cambium temperature closely approximated that of the air.

Two main factors thus were concerned in determining the temperature of the tree at this time of year. The first was the flow of heat from high to low, that is during the day from the environment inward; and the second was the *active* withdrawal of heat from the tree tissues. This latter action, as amply demonstrated in the records, increased and decreased directly with the increasing and decreasing air temperature, and its cause must then be associated with some reaction of the plant to temperature changes. The relative intensity of these two factors determined the exact temperature attained in the tree. With an increase in the air temperature the cooling action increased faster than the transfer of heat inward from the environment, while during a decrease in the air temperature the transfer of heat inward exceeded the cooling action. Early in the day the cambium attained an approximate balance between the two factors and later a balance was also reached in the tree center, resulting in a longer or shorter period of an approximately steady, low temperature. The application of these principles accounts for the details of a typical record such as that of the following.

From 9:00 p. m., July 13, 1934, the usual steady decline in air temperature continued until 1:30 a. m. on July 14, when there was a sharp drop of 9.5° in the air temperature which ended at 6:00 a. m. Meanwhile the center temperature, coincident with the slow decline in air temperature, continued its slow rise of the night period until 1:30 a. m., at the rate of 1.25° in 4.5 hours. From 1:30 a. m. until about 4:15 a. m. it rose 1.25°, thus

increasing the rate to 1.25° C. in 2.75 hours coincident with that of air-temperature decline. This immediate, inverse relationship is also visually shown by the fact that at exactly 1:30 a. m., when the air temperature began its sharp decline, there was a very slight but definite *upward* movement in the record of the tree-center temperature. From 4:30 to 6:00 a. m. the center temperature remained steadily at 24.75° C., when it began its drop in response to the rise in the air temperature. This record of the center temperature, like that of the cambium, indicates the compound character of the tree temperature. At first the heat added to the system, including the flow inward from the outer tissues, exceeded that absorbed through the internal cooling, and the tree temperature rose. From 4:30 a. m., for 2.75 hours, the transfer of heat inward and the cooling effect balanced one another, causing the leveling of the center-temperature line. At 6:00 a. m. the cooling action began to increase, coincidental with the beginning of the rise in air temperature, and became greater than the inward flow of heat. Therefore the center-temperature line shows the beginning of the daily decline which culminated at about 3:45 p. m. and which caused a drop from 24.75° to 18.00° C., or a total decline of 6.75°, while the air temperature was rising from 22.00 to 36.00° C., or a total of 14°. From 3.45 p. m. until about 6:15 p. m. slight but definite fluctuations in the air temperature were inversely reflected in the center temperature. From then on the regular nightly drop in the air temperature was reflected in the rise of temperature in the center of the tree.

During the next 12 days there were similar conditions, often in intensified form, which may be seen in the graph-records and in table III. The tree-center maximum (T_H max.) and the air-temperature minimum (T_A min.) usually occurred at the same time in the early morning, and the tree-center minimum (T_H min.) and the air-temperature maximum (T_A max.) at the same time in the afternoon. However, the maxima and minima often covered considerable periods of time, and for tabulation purposes it was necessary to select some certain point in each of these periods. Because of the instantaneous response of the

tree to changes during the high-temperature period the point of beginning of the air-temperature rise was assumed to mark the point in the tree-temperature maximum when the morning air-temperature rise began to influence the tree temperature. This point then was used as T_H max. and T_A min. The other maximum and minimum points were selected by the application of the same general principle. From tables III and IV it can be

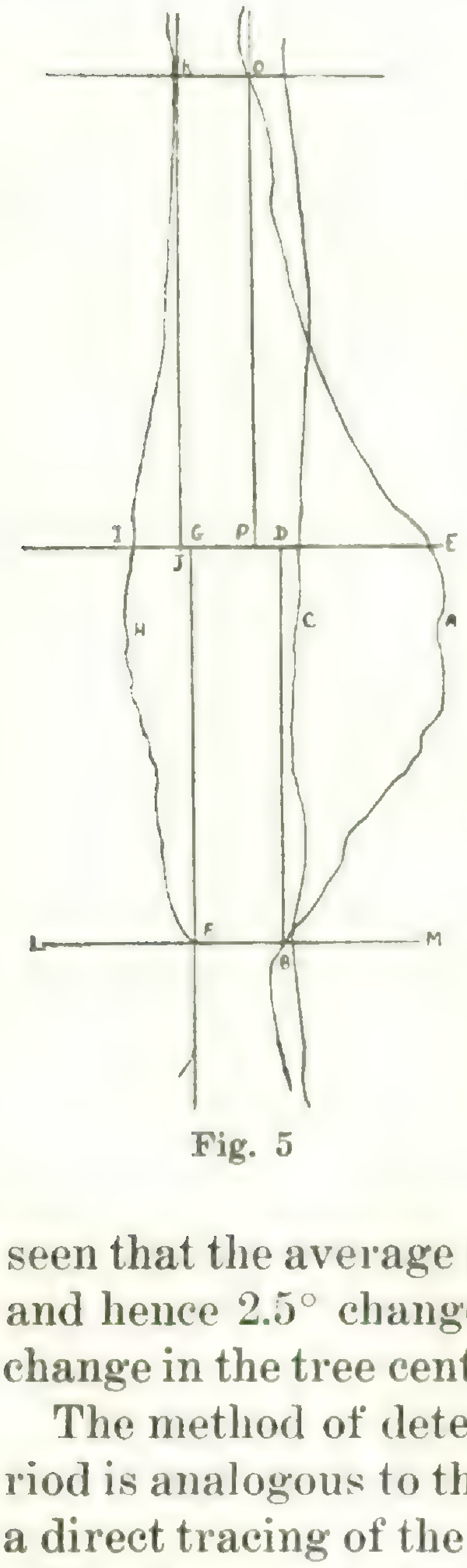

Fig. 5

Fig. 5. Demonstrating method of calculating "degree-hours" for high-temperature period.

BAO is the T_A line; FHK the T_H line; C, the T_C line; LM, the 7 a. m. line; IE, the 3:15 p. m. line, and KO at 5:15 a. m., July 21. The position of IE was fixed by the beginning of the decline in BAO. BAED is taken as the area representing the total heat in "degree-hours" during the air-temperature rise, and FHIG the corresponding number of "degree-hours" of temperature decrease at the tree center. Area PEO represents the total "degree-hour" decline in air temperature to the 5:15 a. m. line, and JIK the corresponding "degree-hours" of temperature rise at the tree center.

seen that the average ratio T_A change/ T_H change was about 2.5 and hence 2.5° change in air temperature caused 1.0° reverse change in the tree center.

The method of determining the "degree-hours" for this period is analogous to that in fig. 4, and is shown in fig. 5, which is a direct tracing of the record for July 20, 1934.

There are two possible explanations of the type of curve found in the record throughout most of July, 1934. The alter-

nating upward and downward movements of the lines might be due to an essentially regular "lag" period of twelve hours, by which the low tree temperatures of one daylight period

TABLE III

COMPARISON OF INFLUENCE OF RISE AND FALL OF AIR TEMPERATURE ON TREE TEMPERATURE

(a) 1934 July	(b) T_H max.*	(c) T_H min.†	(d) T_H change	(e) T_A min.#	(f) T_A max.§	(g) T_A change
Period of air-temperature rise						
14	23.75**	18.25	5.50	23.75**	34.75	11.00
15	22.00	18.25	3.75	25.75	38.50	12.75
16	23.25	19.50	3.75	26.00	37.50	11.50
17	21.75	17.75	4.00	22.75	32.75	10.00
18‡	21.00	15.75	5.25	25.75	37.50	11.75
19	21.50	17.25	4.25	26.75	38.75	12.00
20	22.25	17.00	5.25	28.75	42.00	13.25
21	21.50	17.25	4.25	27.25	39.25	12.00
22	21.50	17.50	4.00	27.25	38.50	11.25
23	21.50	14.75‖	6.75	25.00	36.50	11.50
24	21.50	15.00	6.50	29.00	42.00	13.00
25	20.50	16.25	4.25	29.50	41.50	12.00
26	20.00	19.00	1.00	27.25	30.25	3.00
		Total	58.50			145.00##
Period of air-temperature drop						
14	22.50¶	18.50	4.00	27.25††¶	37.00	9.75
15	23.75	19.25	4.50	27.50	39.00	11.50
16	21.50‖	19.50	2.00	27.50	37.50	10.00
17	21.25	19.00	2.25	26.75	32.00	5.25
18	21.75	15.25	6.50	26.50	39.25	12.75
19	22.25	18.00	4.25	28.75	39.50	10.75
20	21.25	17.25	4.00	29.50	41.50	12.00
21	21.50	17.50	4.00	29.50	40.00	10.50
22	21.75	17.25	4.50	25.50	38.75	13.25
23	21.25	18.25	3.00	32.75	41.75	9.00
24	20.75	16.00	4.75	29.50	42.25	12.75
25	19.50	16.50	3.00	33.00	42.00	9.00
26	18.00	17.00	1.00	30.00	33.25	3.25
		Total	47.75			129.75‡‡

* T_H max. taken at the same time as the end of the T_A min.
† T_H min. taken at the same time as the first point in the T_A max.
\# T_A min. taken at the last low point before the rapid rise in the air temperature.
§ T_A max. taken at the first high point reached by the air temperature in the a. m. rise.
** T_H max. and T_A min. taken at a. m. intersection of T_A with T_H.
‡ Subsequent small changes in air temperature and inverse changes in tree temperature.
‖ 7:30 p. m.
†† T_A min. (for "Temperature drop") taken at the beginning of the steady high temperature of the tree.
¶ T_H max. and T_A min. taken at the first point in the T_H line at which it reached essentially a steady temperature, if not at the absolute T_A min.
\#\# T_A/T_H = 145.00/58.50 = 2.47 :1.
‡‡ T_A/T_H = 129.75/47.75 = 2.71 :1.

TABLE IV

HIGH-TEMPERATURE PERIOD. RATIO BETWEEN AIR-TEMPERATURE CHANGE AND TREE-CENTER TEMPERATURE CHANGE IN "DEGREE-HOURS." THE DIVIDING LINE BETWEEN "UP" AND "DOWN" (E.G. ON JULY 18 AT 3:45 P. M.) TAKEN AT THE BEGINNING POINT IN THE DECLINE OF T_A AND RISE OF T_H

1934 July	Air temp.		Tree temp.		$\frac{T_A \text{ Up}}{T_H \text{ Down}}$	$\frac{T_A \text{ Down}}{T_H \text{ Up}}$
	Up	Down	Down	Up		
14–15	74	34	35	14	$\frac{74}{35} = \frac{2.1}{1}$	$\frac{34}{14} = \frac{2.4}{1}$*
18–19	77	67	31	21	$\frac{77}{31} = \frac{2.5}{1}$	$\frac{67}{21} = \frac{3.2}{1}$†
19–20	72	26	25	12	$\frac{72}{25} = \frac{2.8}{1}$	$\frac{26}{12} = \frac{2.1}{1}$#
20–21	91	33	35	16	$\frac{91}{35} = \frac{2.6}{1}$	$\frac{33}{16} = \frac{2.0}{1}$¶
24–25	116	49	54	20	$\frac{116}{54} = \frac{2.1}{1}$	$\frac{49}{20} = \frac{2.4}{1}$§

* 1st T_A min. and T_H max. at intersection, 7:30 a. m.; 2nd T_A min. and T_H max., 2:30 a. m., 7/15.
† 1st T_A min. and T_H max., 8:15 a. m.; 2nd T_A min. and T_H max., 3:15 a. m., 7/19.
# 1st T_A min. and T_H max., 6:30 a. m.; 2nd T_A min. and T_H max., 12:00 midnight.
¶ 1st T_A min. and T_H max., 7:00 a. m.; 2nd T_A min. and T_H max., 1:30 a. m., 7/21.
§ 1st T_A min. and T_H max., 6:00 a. m.; 2nd T_A min. and T_H max., 4:00 a. m., 7/25.

would be due to the declining air temperature of the preceding night. The only alternate explanation is that the low tree temperatures were due to a definite cooling concurrent with and related to the air-temperature rises of the daylight period. This latter is the hypothesis adopted in the earlier portion of this section. We will now consider the objections to the first of these alternate suggestions.

First, in the earlier part of the year the apparent lags due to rate of heat conduction through the tree tissues were, at the longest, about 1.5 to 2.5 hours, and sharper changes of air temperature caused an evident response even within an hour. Moreover, a study of the records shows that immediately after the intersections of T_A with T_H in the morning and afternoon the temperature usually continued its decline or rise respectively for 0.5 to 1 hour before the change in direction of the T_H

line can be detected. Hence the 1.5- to 2.5-hour lag includes the time when the influence of the preceding temperature was still operating. Actually, then, this apparent lag is longer than the true lag due to the heat conduction rate of the tissue. Second, the records at various seasons of the year show that when there was a deep and long depression of the air temperature below and before the morning intersection of T_A with T_H, especially with a slow rise in air temperature above the intersection, the apparent lag in rise of the tree temperature might be prolonged to 3 to 4 hours. With a shortening and decreasing of the cool period prior to the morning intersection of T_A and T_H the apparent lag period decreased. Therefore when there was no such depression below the tree temperatures, as during the latter part of July, 1934, there would be no apparent lag period and the cooling action would be immediately evident with rise of air temperature. Such was the condition during this hot spell of July, which is strong evidence also that the conditions recorded in the chart could not have been due to a 12-hour lag. Third, since the air temperatures during this entire period were, even at their lowest, higher than the highest point in the tree-center temperatures, a decline in the air temperature could not have lowered the tree-center temperature. Since the first explanation evidently cannot be accepted, the positive evidences in favor of the second alternative will be considered.

In passing from the early portion of the year toward the high-temperature period the apparent morning lag in T_H advanced from about 1.5 hours to about 3.5 hours (table v, column ''d''). This lengthening of the apparent lag period cannot be assumed to be due to an actual change in the heat conductance of the tissues and hence a change in the true lag. Moreover, since the tissues involved are identical for the various years listed, no important difference in conductivity can be due to tissue differences. Therefore, this difference in apparent lag period can only be accounted for on the assumption of a cooling of the tissues which counteracted to a greater or less extent the heat from the rise in the air temperature. Furthermore, the following study of the records of several

TABLE V
INFLUENCE OF COOLING ACTION UPON "LAG"

Beginning of temperature rise*				Beginning of temperature fall					
a	b	c	d	e	f	g	h	i	j
(1930) July†	Air time	Center time	Diff. hours	Air time	Center time	Diff. hours	Air time	Cambium time	Diff. hours
24	10:00 a. m.	1:00 p. m.	3.0	8:30 p. m.	10:30 p. m.	2.0	8:30 p. m.	8:30 p. m.	0.00
25	6:30 a. m.	9:30 a. m.	3.0	10:00 p. m.	12:30 a. m.	2.5	10:00 p. m.	12:30 a. m.	2.5
26	6:45 a. m.	9:00 a. m.	2.25	11:30 p. m.	2:00 a. m.	2.5	11:30 p. m.	12:30 a. m.	1.0
27	7:00 a. m.	10:00 a. m.	3.0	10:45 p. m.	12:30 a. m.	1.75	10:45 p. m.	11:30 p. m.	0.75
28	7:30 a. m.	10:00 a. m.	2.5	11:15 p. m.	1:30 a. m.	2.25	11:15 p. m.	12:00 m.	0.75
(1932) June‡									
10	7:00 a. m.	9:30 a. m.	2.5	10:00 p. m.	12:30 a. m.	2.5	9:30 p. m.	10:00 p. m.	0.5
11	7:30 a. m.	10:30 a. m.	3.0	10:00 p. m.	12:00 p. m.	2.0	9:30 p. m.	10:00 p. m.	0.5
12	8:00 a. m.	11:30 a. m.	3.5	11:00 p. m.	1:00 a. m.	2.0	10:00 p. m.	11:00 p. m.	1.0
(1934) May#									
1	7:30 a. m.	9:00 a. m.	1.5	7:30 p. m.	9:30 p. m.	2.0	6:45 p. m.	7:30 p. m.	0.75
2	7:00 a. m.	8:30 a. m.	1.5	8:00 p. m.	9:15 p. m.	1.25	7:15 p. m.	7:30 p. m.	0.25
3	7:30 a. m.	10:00 a. m.	2.5	9:30 p. m.	11:30 p. m.	2.00	8:00 p. m.	9:30 p. m.	1.50
(1932) May									
13	7:30 a. m.	9:30 a. m.	2.0	11:00 p. m.	1:30 a. m.	2.5	9:45 p. m.	10:30 p. m.	0.75
14	7:00 a. m.	9:30 a. m.	2.5	11:30 p. m.	1:30 p. m.	3.0	10:15 p. m.	11:15 p. m.	1.0
28	8:15 a. m.	9:45 a. m.	1.5	7:00 p. m.	10:00 p. m.	3.0	6:15 p. m.	7:00 p. m.	0.75
29	6:00 a. m.	8:00 a. m.	2.0	8:30 p. m.	10:30 p. m.	2.0	7:00 p. m.	8:00 p. m.	1.0
30	6:30 a. m.	9:00 a. m.	2.5	10:00 p. m.	12:00 p. m.	2.0	8:30 p. m.	9:00 p. m.	0.5

(1934) April									
1	6:00 a. m.	8:30 a. m.	2.5	8:15 p. m.	9:30 p. m.	1.25	7:00 p. m.	8:00 p. m.	1.00
2	7:00 a. m.	8:30 a. m.	1.5	12:00 p. m.	1:30 a. m.	1.50	10:00 p. m.	10:30 p. m.	0.50
3	8:15 a. m.	10:15 a. m.	2.0	8:00 p. m.	9:30 p. m.	1.50	7:00 p. m.	7:30 p. m.	0.50
4	7:30 a. m.	8:30 a. m.	1.0	5:00 p. m.	6:00 p. m.	1.00	5:00 p. m.	5:15 p. m.	0.25
9	7:00 a. m.	8:00 a. m.	1.0	7:30 p. m.	9:30 p. m.	2.00	7:00 p. m.	7:15 p. m.	0.25
10	8:30 a. m.	9:00 a. m.	0.5	8:15 p. m.	9:30 p. m.	1.25	6:30 p. m.	7:30 p. m.	1.0
12	9:00 a. m.	10:30 a. m.	1.5	6:30 p. m.	8:30 p. m.	2.00	5:30 p. m.	6:30 p. m.	1.0
(1932) March									
18	7:45 a. m.	9:30 a. m.	1.75	9:45 p. m.	11:00 p. m.	1.25	7:15 p. m.	8:15 p. m.	1.00
19	8:00 a. m.	9:30 a. m.	1.5	6:15 p. m.	8:30 p. m.	2.25	5:45 p. m.	6:00 p. m.	0.25
20	10:30 a. m.	12:00 m.	1.5	7:30 p. m.	10:00 p. m.	2.50	6:30 p. m.	7:00 p. m.	0.50

* Following the principles indicated under Nos. 2 and 3 of the section on "Methods," the beginning of air-temperature rise and fall is taken at the intersection of T_A with T_H and T_C.

† During the latter part of July, 1930, a considerable cooling action was evident in increasing the "lag" periods, as shown in columns "d" and "g," and to some extent in column "j." On July 29 the tree-center temperature did not rise until after the air temperature began to decline in the p. m., by which time the cooling action was sufficient to neutralize completely the effect of the rise in air temperature.

‡ The same type of record was shown June 10–12, 1932. Before and after these dates definite cooling action was evidenced by the lack of rise in the tree-center temperature during the a. m. rise of the air temperature.

May 4, 5, and 6 show little rise until the p. m. decline in T_A and with T_C closer to T_H than before.

specific cases will give clear evidence of the validity of the concept of a positive cooling action in the tissues, and the difficulty in accounting for the curves on the basis of a "lag" of several to 12 hours.

In early June, 1934 (e.g., June 3, 4, 5, etc.), the maximum temperature of the cambium was reached approximately 2 hours before that of the center, while the air temperature was falling, sometimes even below the tree temperatures, as on June 5 at 12:00–5:30 a. m. The high air temperature preceding the high tree temperature was at about 1:30 p. m., the day before, with a secondary high at 4:30–5:30 p. m. (30° C.), or in other words 10 to 12 hours before. This rise of the tree temperature, both center and cambium, could not be ascribed to "lag" due to slow conduction of heat from the outside, because of the great length of time. Therefore it must be ascribed to an actual warming up of the inner tissues due to the slow removal of the cooling action.

The records show that on May 13 and 14, 1932, there was a period of 1.5 to 2 hours from the morning intersection of T_A with T_H to the beginning of the rise in T_H, while on May 15 there was no rise at all until the afternoon decline in T_A began. The 1.5- to 2-hour period is the usual interim, which represents the maximum true lag in the beginning of the reaction of the tree-center temperature to a change in air temperature. The lack of such a lag period on May 15 indicates that the cooling action within the tree was sufficient to counteract the incoming heat. In other words, due to the cooling action, the 43 "degree-hours" change of the atmosphere was unable to raise the temperature at the center of the tree. On May 14 a 12° rise in the air temperature caused a rise of only two degrees at the tree center while on May 15 a 15.5° rise failed to change the tree-center temperature.

During the night of June 3–4, 1932, the tree-temperature lines and that of the air were superimposed for about 13 hours, and about 5 a. m. the air temperature began a slow rise. At about 8 a. m. the tree-center temperature began to rise, and a total rise of 10.00° in the air temperature resulted in a 1.25°

rise in the tree center. During the next several days the tree-center temperature showed no rise except in association with the afternoon decreases in the air temperature. Here again on the first of these days the cooling action was not quite sufficient to neutralize the heat which penetrated from the atmosphere, while on the several following days it was sufficient. The records for July 13, 14, and 15, 1932, are typical of a large number of those for that month, which show that the cooling action was sufficient to prevent any heating of the tree center. During most of this period the cambium temperature was held at 1 to 2° above the center temperature, with little evidence of being influenced by the air temperature. This condition contrasts with that in March and April, as, for example, April 29, 1934, where the cambium temperature was influenced much more by that of the air and averaged 3° or more above that of the tree center. Even at this time, however, there was probably a considerable cooling action, since a few days later, by May 3 and 4, there was only a slight rise of temperature in the tree center. The record of March 19, 1932, illustrates the relationship of the three lines when little affected by the cooling action within the tree. Here there was an average difference between the T_H and T_C lines of about 4°, and the T_C line was almost in mid-position between the T_H and T_A lines.

A comparison of the spread of the three temperature lines during the latter part of June and the month of July, 1934, (table VI) shows that in general while the distance between the air-temperature and the tree-center-temperature lines (T_A max. minus T_H min.) increased greatly with the hotter weather, the distance between the air-temperature and the cambium-temperature lines (T_A max. minus T_C) averaged about the same throughout the whole period. Since, moreover, the distance between the two tree temperature lines (T_C minus T_H min.) increased greatly, the cooling action must have increased much more at the center than at the cambium. That the center cold zone was somewhat more effective in cooling the cambium at high temperatures than at lower ones is shown by the fact that there was a greater increase in the air temperature from

the early part of the period to the latter part than there was in the cambium temperature.

TABLE VI

T_H MIN., T_A MAX., AND T_C AVERAGE, JUNE AND JULY, 1934*

(1934) June	T_H min.	T_A max.	T_C average	Diff. T_A max. and T_H min.	Diff. T_A max. and T_C	Diff. T_C¶ and T_H min.
19**	19.5–21.5	31.75	20.00–24.00	11.25	9.75	1.5
20**	21.5–23.0	33.50	22.50–25.25	11.25	10.25	2.0
21	23.25	33.00	25.00	9.75	8.00	1.75
22	23.25	34.00	25.00	10.75	9.00	1.75
23	24.75–25.25	37.00	26.25	12.00	10.75	1.25
24	25.00	36.00	27.00	11.00	9.00	2.00
25	24.50	35.75	26.50	11.25	9.25	2.00
26	25.00	36.25	27.00	11.25	9.25	2.00
27	25.50–25.75	37.75	27.75	12.00	10.00	2.00+
28	25.75	37.75	27.75	12.00	10.00	2.00
29	26.00	38.00	28.00	12.00	10.00	2.00
30	irregular		26.25			
July						
1†‡	21.50	33.50	25.00	12.00	8.50	3.50
2	20.75	36.00	26.00–27.25	15.25	9.50	5.75
3#	19.00	37.00	26.75–27.50	18.00	10.00	8.00
4	18.00	36.00	27.00–27.75	18.00	8.50	9.25
5	18.00	36.50	28.00	18.50	8.50	10.00
6	19.50	29.00				
		irregular	27.00	9.50	2.00	7.50
7†	17.75	31.00	26.00	13.25	5.00	8.25
8	17.25	31.50	25.75–26.75	14.25	6.25	9.00
9†	20.50	32.00	26.00–27.00	11.50	5.50	5.75
10	18.00	34.25	25.00–28.00	16.25	7.75	8.50
11	20.00	37.00	27.50–31.00	17.00	7.75	9.25
12	19.75	39.50	27.50–31.00	19.75	10.25	9.50
13	18.75	39.50	29.25–31.00	20.75	9.25	11.50
14	18.00	36.75	27.50–29.25	18.75	8.75	10.25
15	18.00	38.75	28.50–30.50	20.75	9.25	11.00
16	19.50	37.00	29.50–30.00	17.50	7.25	10.25
17	17.75	32.25	28.25	14.50	4.00	10.50
18	16.75	38.75	27.75–30.75	22.00	10.00	12.50
19	17.50	39.25	29.25–30.75	21.75	9.75	12.50
20	16.50	42.00	30.50–31.75	25.50	11.00	14.50
21	17.00	40.00	30.25–31.50	23.00	9.25	13.50
22	17.50	38.75	30.25–31.00	21.25	8.25	13.25
23	15.50	41.50	29.25–32.00	26.00	11.00	15.00
24	15.25	42.00	31.25–32.25	26.75	10.25	16.50
25	16.00	42.00	31.25–32.25	26.00	10.25	15.75
26	17.00	32.75	29.50	15.75	3.25	12.50

* In degrees centigrade.
** Both T_H and T_C rise with T_A.
† Slight a. m. intersection of T_A with T_H.
‡ T_C farther from T_H.
# No a. m. intersection of T_A with T_H.
¶ Intermediate values sometimes used for T_C.

On July 16, 1934, at 7:00–7:30 p. m., a sharp drop in the atmospheric temperature not only resulted in a sharp rise in the tree-center temperature but also in about a 0.5° temporary rise in the cambium temperature. This was immediately followed by a decline in the latter as the air temperature dropped. The immediate inverse response in the tree to air-temperature change definitely indicates the instantaneous nature of the thermostatic action. Often, even in minor fluctuations, this is shown in the records of the high temperature period (table VII).

TABLE VII

EXAMPLES OF MINOR, INVERSE REACTIONS TO TEMPERATURE CHANGES

(1934) July	Hour	Air-temperature change	Tree-temperature changes	Notes
14	9:30–10:00 a. m.	1.5° decline	Cambium and center rise	
	5:30–6:00 p. m.	Slight rise	Slight center drop	
15	1:30 p. m.	1.0° rise	1.0° drop	
16	10:00–11:30 a. m.	3.5° rise	1.0° center drop 0.5° cambium drop	Further air-temperature and center change
17	4:00–6:00 a. m.	2.25° drop and then a. m. rise	About 0.5° rise and then a. m. drop	Several further minor fluctuations
18	10:30–11:30 a. m.	6.5° rise	3.0° center drop	Several further fluctuations and reverse responses
19		Several fluctuations	Several reverse responses in center	
24	11:00–11:30 a. m.	Sharp increase in temp. rise	Sharp drop 1.5° center	
	3:30–4:30 p. m.	Sharp drop and rise	Sharp rise and drop in center and slight effect on cambium	

On each of these days also the beginnings of the rapid morning rise of air temperature and of afternoon decline are associated with immediate reverse changes in the tree temperatures, so that in general the T_H line is usually a mirror image of the T_A line. These examples not only clearly indicate the almost

instantaneous nature of the thermostatic action, but also give positive evidence that the active cooling of the tissues is a response to the air-temperature rise.

After considering the various positive evidences just cited it can hardly be doubted but that thermostatic cooling is a major factor in determining the tree temperatures during the high-temperature periods of the year. Other phenomena associated with the summer periods will now be considered.

The morning sharp rise in the cambium temperature, during this period, which parallels that of the air temperature, may be due to either one of two factors or a combination of them. It may be assumed that in the morning a certain amount of direct insolation of the tree trunk might have taken place in spite of its being shaded by the heavy foliage. There are no direct observations upon this point. On the other hand, it may be assumed that the sharp rise in air temperature generally caused the corresponding rise in the cambium temperature. It appears from a tabulation that these sharp rises in the cambium temperature began essentially at the same time, about 7:30 each morning. Direct insolation could have been the cause, since the sun's rays would have been at the same angle each day over this short period of time.

On the other hand, there was a direct relationship between the intersection point and the beginning of the rise in T_c, usually a 15-minute interval only, which coincides with the lag in cambium-temperature at other times in the day and other seasons of the year when direct insolation would be impossible. There is then no conclusive evidence on this point, although the case next cited indicates direct insolation as a factor at this time of day.

The cambium temperature during the night of July 13–14, 1934, began a slow decline at about 11 p. m., which continued until about 4 a. m., when a 3° drop in 3.5 hours occurred, resulting from an almost synchronous sharp drop in the air from 27.75 to 22.00° C. Incidentally it may be noted that there was a "lag" of about 15 minutes between the beginning of the sharp drop in the temperature of the air and the beginning of the 3°

drop in the cambium region. From 7:30 a. m. until about 10:15 a. m., this region remained steadily at about 28.25° C. Since both the air and center had lower temperatures the cambium should have continued to drop due to continued radiation of heat to them. That it did not do so is indicative that a source of heat sufficient to balance the radiation from the cambium must have been present. Direct insolation is thus suggested.

It will be evident from the following discussion that thermostasy was not confined to the excessively hot dry period of late July in 1934. An intermediate condition is shown on the record for July 14, 1934, when the air temperature dropped below that of the tree center for approximately 3 hours during the early morning. Except for this early morning drop, the record is essentially like those which followed it. The T_H line began to drop from 25.00° C. about 1.75 hours after the T_A line first crossed the T_H line, at which time the temperature of the air fell below that of the tree center. For about 1.25 hours the tree-center temperature dropped in response to the lower air temperature. Then the T_A line re-crossed the T_H line due to the daily rise in air temperature. After that the T_H line continued its downward course, but now the decreasing center temperature was due mainly to the thermostatic action associated with the rising air temperature. That this decreasing tree temperature is due to one factor in part of the curve and to another factor in another part emphasizes both the necessity of a careful analysis of the records and one cause of misinterpretation of former records in which intermittent and partly correlated observations were made.

On July 2, 1934, about 5 a. m., the air temperature dropped somewhat below that of the tree center and under its influence the latter continued to decline. At 7 a. m. the air-temperature line re-crossed that of the center temperature, which continued to drop with a slight acceleration until 10 a. m. This decline may perhaps be considered as due to: (1) the "lag" in response to the former air-temperature decline, and (2) an acceleration of this drop due to thermostasy. That the latter is a real factor can be seen from the further changes of the two temperatures.

From 9 to 10:30 a. m. the air temperature was almost steady, though with a drop of 1° during the last 0.75 hour. At about 10:30 the center line leveled out, thus showing that the flow of heat in from the heated air and out through the cooling action had attained a temporary equilibrium. When at 11:30 the air temperature began to rise again the center temperature responded by a slow decline of 0.50°, beginning about 0.5 hour later. A decline of air temperature of 2° in 1.5 hours, beginning at 1 p. m., was registered an hour later in the center by the beginning of a rise of nearly 0.5°. The air-temperature rise, starting at 2:30 p. m., was reflected in the center an hour later by the beginning of a decline of 1.25°. The final decline in air temperature for the day began at about 5:15 p. m., and the final rise of the center temperature began about an hour later. This analysis of the fluctuations in the day's records shows that there was a "lag" of about one hour in the response of the tree center to air-temperature changes. It should be clearly understood that this type of "lag" is in no way similar to the "lag" which may be due to slow conduction of heat into or out of the tree. At a later stage in the water deficit in the tree (July 15–30) there was essentially no lag in this internal thermostatic action.

On July 26–28, 1930, the temperature reached a maximum each day of 39–41° C., following a long period of medium-high temperatures with maxima between 25 and 35° C. The tree temperatures during the earlier period had varied plus or minus 1 to 2° around 25° C. During the 3-day period under consideration this variation had shifted to plus or minus 1 to 2° around 30° C., with the center during the maximum periods about 2° lower than the cambium. Two additional phenomena are especially notable during this period. First, when the air temperature was at its maximum, the center temperature was approximately 10° below it, and its own maximum was 7 or more degrees below the air maximum. Second, on the third day, which was the hottest, the center and cambium regions were both cooler than on the preceding day as evidenced in table VIII.

TABLE VIII

(1930) July	Time	Max. air temperature	Tree-center temperature	Tree-cambium temperature	Degree-hours between 30° line and air-temperature line
26	3:00 p. m. 5:00 p. m. 9:45 p. m.	38.75° C.	29.75° C. 31.25° C.	31.50° C. 32.00° C.	82
27	3:00 p. m. 5:30 p. m. 11:00 p. m.	40° C.	30° C 31.25° C.	31.75° C. 32.00–° C.	95
28	3:30 p. m. 5:30 p. m. 11:00 p. m.	41° C.	29.75° C. 31.25° C.	31.50° C. 31.75° C.	103

In addition, although the maximum air temperature on July 28 was 2.25° higher and there were 21 more "degree-hours" of change than on July 26, the tree temperatures were the same on both days. This indicates clearly that during the summer period of 1930 the same cooling action which was so sharply evident during the excessively hot dry spell of 1934 was effective in keeping the tree temperatures well below those of the air. It should be noted again that since during periods of low to moderate air temperatures the tree-temperature graphs often are almost superimposed upon that of the air, at higher temperatures a great resistance is evidently offered by the tree tissues to increase of temperature. This cannot be due to slow conduction of heat through the tissues, since in this set of observations the same set of tissues was involved throughout, and relatively rapid response, together with a temperature essentially equal to that of the air, was very frequent. The "lag" which has been heretofore ascribed to slow heat conduction and heat radiation is therefore due not only to these factors in part, but also to this thermostatic cooling of the tissues.

During large portions of July and August, 1932, both tree temperatures held steadily between 25 and 30° C., with only slight movement up and down in response to the daily and nightly swings of 10° in the air temperature. This resistance by the tree to change of temperature during considerable

changes in air temperature may now definitely be ascribed to the thermostatic action and not mainly to "lag" induced by slow heat conduction.

On July 29, 1930, the cooling effect on the tree temperatures is shown by the fact that, following the intersection of T_A with T_H and T_C during the morning rise of T_A, the line representing T_H dropped as T_A increased and the rise in T_C was postponed for 3 hours, until 12:30 p. m. During the preceding days it had varied only from 0.25 to 0.75 hour later than the intersection of T_A and T_C. For the entire period of July 23–28, 1930, an increased cooling action in the tree is evidenced by the increase of the difference between the tree-temperature maxima and the air-temperature maximum as seen in table IX.

TABLE IX

(1930) July	T_A max.	T_H max.	Diff. T_A and T_H	T_C max.	Diff. T_A and T_C
23	31.50	26.25	5.25°	26.75	4.75°
24	30.00	25.75	4.25°	26.00	4.00°
25	36.00	27.75	8.25°	28.75	7.25°
26	38.75	31.25	7.50°	31.75	7.00°
27	40.00	31.00	9.00°	31.75	8.25°
28	41.00–	31.25–	9.75°	31.75	9.25°
29	33.75	28.25	5.50°	29.00	4.75°

For all of these periods, during which a definite thermostatic cooling can be demonstrated, the number of "degree-hours" of air-temperature rise required to cause one "degree-hour" rise in the tree center is indicated in table X. In general, it can be seen that the ratio rises from about 3:1, when the cooling action due to transpiration would be none or slight, to much higher ratios as the season advances until in certain cases little or no rise takes place in the tree in response to the rise in air temperature. The next step is the positive reduction of tree temperature during the air-temperature rises. The variability in the ratios may be accounted for by the action of other factors than air temperature as discussed in a later section.

It is clear from the records just cited that the thermostatic cooling of the tree tissues is a phenomenon present at least dur-

ing the warm portions of the year and not simply under the extreme temperature conditions such as existed in the latter portion of July, 1934.

TABLE X

DEGREE-HOUR RATIOS AT VARIOUS SEASONS OF THE YEAR*

(1934) March	ABD	EFG	Ratio ABD/EFG	T_A max.	
15	83	29	2.8:1	15.50° C.	2 hrs.
16	42	16	2.6:1	17.00° C.	2 hrs.
17	37	10	3.7:1	22.00° C.	2 hrs.
29	87	30	2.9:1	19.00° C.	2 hrs.
30	55	14	3.9:1	22.25° C.	3 hrs.
April					
1	72	24	3:1	18.00° C.	5 hrs.
2	93	30	3.1:1	24.50° C.	3 hrs.
14	94	34	2.4:1	23.50° C.	2 hrs.
16	58	16	3.6:1	20.00° C.	2 hrs.
17	52	18	2.9:1	20.00° C.	3 hrs.
18	69	25	2.7:1	26.50° C.	2.5 hrs
23	76	19	4.0:1	27.00° C.	1.75 hrs.
25	39	9	4.3:1	20.00° C.	1 hr.
27	21	7	3:1	15.00° C.	2 hrs.
28	51	15	3.4:1	18.50° C.	2 hrs.
29	63	18	3.5:1	24.00° C.	1.5 hrs.
May					
3	44	8	5.1:1	27.50° C.	2 hrs.
6†	66	9	7.3:1	29.00° C.	1 hr.
7†					
8†	40	1	40.0:1	29.50° C.	2 hrs.
9†	71	3	23.0:1	33.25° C.	2.5 hrs.
12	53	10	5.3:1	28.25° C.	2 hrs.
16	66	16	4.1:1	24.00° C.	3 hrs.
17	69	15	4.6:1	28.50° C.	1.5 hrs.
18†	69	9	7.6:1	29.50° C.	1 hr.
19–22†					
23	50	10	5:1	26.75° C.	2 hrs.
25	29	10	2.9:1	21.50° C.	1.5 hrs.
26	58	15	3.8:1	23.75° C.	1.5 hrs.
27	75	15	5.0:1	26.25° C.	4 hrs.
28	129	23	5.6:1	29.25° C.	2.5 hrs.
29	100	13	7.7:1	33.00° C.	2 hrs.
30†					
31†					
June					
3†					

* In calculating these areas the boundary of the tree temperature area was raised 1.5 hours to make up for the 1.5-hour "lag" approximately, which occurs in the initiation of the rise of the tree temperature after the intersection of the T_A with the T_H line during the morning rise of T. 1.5 hours past the *last point* of air maximum taken as line FG. (See fig. 4.)

† Shows inverse relation of T_H to T_A in p. m.

TABLE X—(Continued)

(1932) June	ABD	EFG	Ratio $\frac{ABD}{EFG}$	T_A max.
12	45	5	9:1	
13	28	4	7:1	
14	16	1	16:1	
15	33	4	8.2:1	
16	59	6	10:1	
17	63	7	9:1	
29	63	10	6.3:1	
July				
14	55	2	27.5:1	
15	56	3	18.7:1	
(1930) July				
24	23	5	4.6:1	
26	74	15	5:1	
27	69	7	9.8:1	
28	66	5	13.2:1	
29	24	1	24:1	

MEDIUM TEMPERATURES

Many of the principles previously discussed are applicable to the medium range of temperatures, and some "case studies" in this range were necessarily considered in former sections of this paper. The demonstration of thermostasy in this temperature range is important as indicating that it is a general phenomenon which is one of the significant factors determining the tree temperatures.

Evident cooling of both center and cambium tissues, associated with air-temperature increases, shows clearly on the record of early July, 1934, when both failed to follow the upward trend of the air temperature and when the center temperature had even a slight downward trend. The thermostatic action is visually demonstrated in an especially striking manner on July 5, when at 2 p. m. a sharp *drop* in the air temperature of almost 5.0° was reflected immediately in a sharp *rise* of the center temperature of slightly over 0.5°. This contrasts sharply with the normal condition at periods of the year when foliage and therefore active transpiration are absent.

EARLY EVIDENCES OF THERMOSTASY IN 1934

Between 6:15 and 6:30 p. m., June 17, 1934, there was a sharp drop in the air temperature from 30.25 to 19.50° C. At the same time the center and the cambium temperatures took an upward trend, the latter somewhat more marked. This was followed by a general downward movement, the center beginning 1.5 hours after T_A crossed T_H, associated with the continued drop in the air temperature. Two things are shown at this date: (1) the direct and immediate dependence of a rise in the tree temperatures on a drop in the air temperature, and hence the presence of a prior cooling action; and (2) an interval of only 1.5 hours between the intersection of the air line with the tree-center line and the beginning of the decline of the tree-center temperature.

In the latter part of June, 1934, as, for example, June 26, a balance was evident between the transfer of heat inward and the heat removed by the cooling action. From 7 a. m. to 5 p. m. a temperature of 25° C. was steadily maintained in the center of the tree while the air temperature increased from 25° to 36.25° C. in six hours and remained at about that point for 4 hours. At 5 p. m. the air temperature began to drop and simultaneously the tree-center temperature began to rise. This same reaction is traceable through the records of many days from early in May onward through June and July. At this period of the year the daily downward tendency of tree-center temperature usually began coincidentally with the rise in the air temperature. However, when the air temperature dropped for a few hours below that of the tree center, as, for example, from 1:00 to 7:00 a. m. on June 22, there was at times a slow drop in the tree temperatures. This downward movement, due to air cooling, frequently merged into the cooling associated with the rise in the air temperature, but the latter caused an acceleration in the rate of cooling. Thus, on June 22 the rate of cooling just prior to the intersection of the air line with the center line was 0.5° in 2 hours, while immediately following this intersection it was 0.5° in less than an hour. During the latter part of June the period of steady low temperature in the tree center

became longer, indicating an increasing amount of cooling action with the advance of the season.

On June 1, 3, and 4, 1934, a sharp drop and subsequent rise in air temperature occurred each afternoon, and at the same time a small bend upward and downward in the tree-temperature lines appeared. These inverse responses to air temperature changes are identical in type with those which occurred during the high-temperature period of the latter part of July, and indicate clearly the concurrent nature of the air-temperature changes and the inverse tree-temperature changes.

For several hours on June 26 and 27 the air temperature was maintained at 36 and 37° C., which was as high as on some of the days during the later period of July. Yet the cooling of the center of the tree was much less marked, which shows that high temperature alone was not sufficient to occasion the excessive thermostatic action of July, 1934. At air temperatures which averaged below 35° C., as in a long period prior to June 26, the two tree temperatures were very close, usually not more than 2° apart, thus giving evidence of thermostatic cooling of the cambium. On several days during May (6–9, 18–22, 30 and 31), 1934, the tree-temperature line showed definitely a greater rate of increase at about the point on the air-temperature line where the afternoon decrease began. For some of these days also it is impossible to calculate a ratio between the T_A rise and T_H rise, since no evident increase in tree temperature took place until this afternoon inflection of the two lines showed on the record. This lack of rise in the tree temperature in the early part of the day, at the time that the air temperature was increasing, can only be explained by a cooling action within the tree associated with increasing air temperature, and the rise at the time of the air-temperature decrease must be due to a decreasing cooling action associated with decreasing air temperatures. This may be demonstrated also in the following manner. The period of temperature rise in the tree center may be divided into two portions, the first, up to the time of the beginning of the afternoon decline in the air temperature, and the second after that time. During the first portion the increasing

air temperature, if there were no concurrent cooling action, should have caused a more rapid rise in the tree temperature than during the second, when the air temperature was actually falling. If the rate of rise in the tree temperature was greater in the second than in the first portion it would indicate an excess of cooling action during the first portion of the curve. The following data for several of the days in May, 1934, thus clearly indicate thermostatic cooling at this period.

May 3—T_H minimum, 19.25° C. at 9:30 a. m.
T_H at 4:30 p. m., 21.25° C. or 2.0° rise in 7 hours.
T_H at 9:00 p. m., 22.00° C. or 0.75° rise in 4.5 hours.
Rate during 1st portion of rise, .28° C. per hour.
Rate during 2nd portion of rise, .16° C. per hour.

Here it is evident there was no excess cooling action, since the rate in the latter portion of the curve was much less than during the first portion. The values for other days in May, calculated in similar fashion, are listed below:

May 4—Rate 1st portion of curve, 0.05° per hour.
Rate 2nd portion of curve, 0.25° per hour.
May 6—Rate 1st portion of curve, 0.11° per hour.
Rate 2nd portion of curve, 0.25° per hour.
May 8—Rate 1st portion of curve, no rise discernible.
Rate 2nd portion of curve, 0.17° per hour.
May 9—Rate 1st portion of curve, 0.11° per hour.
Rate 2nd portion of curve, 0.25° per hour.
May 29—Rate 1st portion of curve, 0.33° per hour.
Rate 2nd portion of curve, 0.41° per hour.

Considerable rates of increase are therefore evident on May 4, 6, 8, 9, and 29, during the second portions of the curves, thus indicating cooling action during the first portion.

The record for May 31, 1934, may be studied as a typical example during the portion of the year when medium temperatures dominated and the thermostatic cooling definitely affected the tree temperatures (table XI derived from the graph-record). The beginning of the rise in air temperature and the

beginning of the daily increase in the rate of decline in the tree temperatures were coincident, at about 5:30 a. m. From about 8:30 a. m. to 5:00 p. m. the tree center remained steadily at 22.75° C., and the cambium slowly rose from 24.50 to 24.75° C. At 5:00 p. m. the air temperature began its usual decline and simultaneously the tree temperatures began to rise, for one hour very slowly and then more rapidly.

TABLE XI

DATA FOR RECORD OF MAY 31, 1934

Item	Time	Temp. ° C.	Rate per hour
1. 1st T_A min.	5:30 a. m.	22.00	
2. 1st intersection of T_A and T_H	6:30 a. m.	24.00	
3. T_H min. (beginning)	12:15 p. m.	22.75	
4. T_A max. (beginning)	12:15 p. m.	35.00	
5. T_A max. (end)	5:00 p. m.	35.50	
6. Beginning 2nd phase of p. m. rise in T_H	6:30 p. m.	23.00	
7. 2nd intersection T_A and T_H	1:30 a.m. 6/1	25.50	
8. T_C min.	8 a. m.–5 p. m.	24.25–24.75	
9. 2nd intersection T_C and T_A	11:15 p. m.	26.75	
10. 2nd T_C max.	12:00 p. m.	26.75	
11. Beginning 1st phase p. m. rise in T_H	5:00 p. m.	22.75	
12. Beginning 1st phase p. m. rise in T_C	5:00 p. m.	24.75	
13. Beginning 2nd phase p. m. rise in T_C	6:00 p. m.	25.00	
14. Beginning 2nd phase p. m. decline in T_H	6:30 p. m.	32.50	
15. a. m. rise in T_A 4 minus 2	5.75 hrs.	11.00	1.91
16. Length of T_A max. 4 to 5	4.75 hrs.		
17. a. m. decline in T_H 2 minus 3	5.75 hrs.	1.25	0.21
18. p. m. decline in T_A 5 minus 11	8.50 hrs.	10.00	1.17
19. Total rise in T_H 7 minus 3	13.25 hrs.	2.75	0.20
20. 1st phase p. m. rise in T_H 11 minus 6	1.5 hrs.	0.25	0.166
21. 2nd phase p. m. rise in T_H 7 minus 6	7.0 hrs.	2.50	0.357
22. 1st period p. m. decline in T_A 5 minus 14	1.5 hrs.	3.00	2.000
23. 2nd period p. m. decline in T_A 14 minus 7	7.0 hrs.	7.00	1.000
24. 1st phase p. m. rise in T_C 13 minus 12	1.0 hrs.	0.25	0.250
25. 2nd phase p. m. rise in T_C 9 minus 13	5.25 hrs.	1.75	0.333

An inspection of the graph-record shows a small but definite bending downward of the tree-temperature lines at 5:30 a. m. coincidental with the beginning of the rise in the air temperature. This demonstrates an increase in thermostatic cooling when the air temperature was relatively low (i.e. 22.00° C.)

and below the tree temperatures, and shows that the cooling action was not necessarily associated with high temperatures. From the data in table XI it is evident that the rise in temperature of the tree, associated with the decline in the air temperature, occurred in two stages. During the first, while the air temperature was dropping at the rate of 2.0° an hour, the center and cambium rose at the rates of 0.166° and 0.25° an hour respectively. During the second phase, when the air-temperature rate of decline was 1.0° an hour, the center and cambium temperature rose 0.357° and 0.333° an hour respectively. Since it cannot be assumed that the rate of heat conduction increased, the data cited above demonstrate that the thermostatic cooling was more effective at higher air temperatures.

On June 17, 1934, from 6:00 a. m. to 3:30 p. m., there was a slow downward movement of the tree-center temperature from 26.00 to 25.00° C., almost coincidental with an increase in air temperature from 24.50° C. at 5:30 a. m. to 31.75° C. at 10:30 a. m., followed by sharp depressions and rises until about 6:15 p. m. At this time a sharp drop from 30.25 to 21.00° C. resulted in an immediate small swerve upward in the center temperature of about 0.5° and in the cambium of about 0.75° C. At about 3:00 p. m. both tree temperatures showed a small but distinct swerve downward in response to an increase in the air temperature from 25.00 to 31.25° C. About 0.5 hour after the intersection of T_A with T_C and 1.0 hour after the intersection of T_A with T_H in the afternoon the T_C and T_H lines began a slow decline in response to the lower air temperature. This was due to heat conduction outward from the tissues.

The record for June 17 emphasizes a number of important points. (1) At this date, well before the hot dry period of late July, the thermostatic action can be seen, not only from the calculations given in table XII but also from the curve where sharp changes in the air temperature occurred. (2) The compound character of the tree temperature due in part to heat gradients across the tissues and in part to the thermostatic cooling action is indicated. (3) That the temperature of the cambium, as well as that of the center, is in part due to a local

cooling of the tissues is demonstrated by the almost immediate reduction of the cambium temperature concurrent with the rapid increase in the air temperature and vice versa. (4) The phenomenon heretofore called "lag" is not simply due to slow conduction of heat into or out of and across the tissues as has been explained by other investigators. This can be demonstrated by a comparison of this record with the records for previous days, as indicated in table XII. On June 14, 15, and 16, for example, there was for each day an interval of from 10 to 12 hours between the middle of the maximum-temperature period of the air and the middle of the maximum-temperature period of the tree center. This formerly has been designated as a "lag" of 10 to 12 hours and ascribed to slow conduction of heat. On June 17, between 5:00 and 7:30 p. m., the sharp drop in air temperature, with mid-point at about 6:30, had its maximum effect upon the cambium and the center of the tree at 7:00 and 8:00 p. m. respectively, or 0.5 hour and 1.5 hours afterwards. Then the cooling action due to the lower air temperature began to reduce the tree temperatures. These intervals of 0.5 and 1.5 hours constitute a partial measure of the true "lag" in the usually accepted sense of that word. A heat gradient from the inner to the outer tissues sufficient to cause the beginning of a detectable decline in the center temperature was attained in about 1.5 hours. However, if an internal thermostatic cooling was taking place, then a decrease in the rate of this cooling due to decline in the air temperature would tend to neutralize for a while the loss of heat to the outside and thus extend the time before the beginning of the decline in the tree temperature. Hence the 0.5 hour and 1.5 hours represent more than the maximum which, under these circumstances, we should assign as the true "lag" period due to slow heat conduction. It is evident, in any case, that since there was little or no rise in T_H while T_A was at its maximum, the 10–12-hour difference between the maximum of the air and that of the tree center on June 14, 15, and 16 could not be due primarily to a slow conduction of heat inward across the tissues, but to a reduction in the cooling action.

TABLE XII

"LAG" BETWEEN T_A MAX. AND T_H MAX., JUNE, 1934

(1934) June	T_A max.*	T_H max.*	Diff. degrees	T_A max. time day	T_H max. time night	Diff. time
11	29.50†	23.75‡	5.75	1:30–5:30	1–3	10.5 hrs.
12	27.25‡	22.50‡	4.75	4:00–5:30	10:30–1:00	5 hrs.
13	29.75†	23.00‡	6.75	1:00–5:00	11–2	9 hrs.
14	28.75†	24.00‡	4.75	1:30–6:00	12:30–2:30	10 hrs.
15	31.75†	25.00‡	6.75	1:00–4:00	1:30–3:30	12 hrs.
16	33.25†	26.25‡	7.00	1:30–5:00	1:30–5:00	12 hrs.

* T_A max. and T_H max. taken as: † central line through a several-hour period of less than 0.50° variation, or ‡ the maximum held for more than 1 hour.

From the cases cited it is evident that at least during the period from early May, 1934, onward there was a thermostatic cooling which often was sufficient to more than overcome the effect of the heat from without. The cases cited will show that this phenomenon was associated not only with the year 1934, when there were exceptional conditions of heat and dryness, but also with other years under moderate temperature conditions.

In 1932 the thermostatic action is traceable back through July and June (at least to June 4) by the actual drop in the center temperature with the morning rise in the air temperature, and by the very slow concurrent rise in the cambium temperature. The latter also showed even on June 4 an accelerated upward movement when the air temperature began to drop.

During periods of moderate fluctuation of the air temperature, e.g., between 15° and 25° or 30° C., as during much of the month of May, 1934, the cambium and center temperatures usually kept within 1 to 2 degrees of each other, with the cambium usually a little higher. The rise and decline of the tree temperatures usually began within less than 2 hours after the intersections of the air-temperature line with the tree-temperature lines, the cambium temperature responding most rapidly. It has already been pointed out that when the tree temperatures were within 2 degrees of each other and the air temperature several degrees above that of the cambium a certain amount of thermostatic cooling was indicated. Usually

this type of record merged a few days later into that in which thermostasy was indicated by a long "lag" period between the morning intersection of T_A with T_H and the beginning in the rise of the tree-center temperature. The various stages in increasing thermostasy during the early part of the season can be seen by comparing successively the records of April 20, 24, 30, May 3, 4, and 5, 1932. On April 20 there was no evidence of cooling action, since (1) the T_H line began its rise 1.5 hours after the morning intersection of T_A with T_H; (2) the T_C line followed closely the rise in T_A and at least 4.0° above the T_H line; and (3) there was no inverse reaction of the T_C and T_H lines at the beginning of the T_A decline in the afternoon. On April 24 (1) the somewhat longer interval, about 2.25 hours, between the intersection of T_A with T_H and the beginning of the rise in T_H, and (2) the somewhat closer approach of the T_C to the T_H line, suggest a slight thermostatic action. A somewhat more pronounced, similar condition on April 30 and May 3 is further indication of increasing cooling action. On May 4 (1) the 3-hour morning postponement in the rise of T_H, (2) the slow rise of T_H and T_C, with a several-hour (ca. 6 hours) flattening of the T_C curve, during the rise in T_A, (3) the close paralleling of T_C with T_H, (4) the distinct rise in T_C concurrent with the decline in T_A, and (5) the inflexing of the T_H line as well, during the decline in T_A, all give clear evidence of thermostatic cooling at this time. All of these features are further strengthened in the record of May 5.

In this series of records thermostasy occurred at moderate air temperatures, with maxima around 30.0° C. for only short periods of the day. An inspection of the graph-records, however, will show that in general there was, through this period, an increasing amount of heat each day, as indicated by the greater area in the chart covered by the T_A line in the later days.

The normal direct reaction of the tree temperatures to changes in the air temperature, as shown in the cases cited below, contrasts in certain definite ways with the indirect thermostatic reaction just illustrated.

The records for March 18 and 19, 1932, are typical of the relationship of the three temperature lines at a time when the tree temperatures were not complicated by transpiration in the tree or by the zero-line adjustments. The cambium temperature was about 4 degrees higher than that of the tree center and was nearly halfway between that of the air and of the tree center. This may be used as one criterion for judging when cooling action became somewhat effective in retarding the direct influence of the atmospheric temperature upon the tree temperatures.

The fluctuations of 12.0 to 15.0° between the night and day air temperatures resulted in almost parallel advances and declines in the tree temperatures, with the latter below the air temperatures from about 8 a. m. to about 6 to 7 p. m., and above them during the night. The beginning of rise in the center temperature on March 19 was about 1.5 hours after the morning intersection of T_A with T_H. The center temperature attained its maximum 1.5 hours after the afternoon intersection of T_A with T_H.

On March 17, 1934, before foliage had developed, there was a sharp drop in the T_A line from 21.5 to 11.5° C. in about 0.75 hour. The T_H line continued its upward movement 0.5° above the intersection of T_A with T_H for about 0.5 hour, and the T_C line continued less than 0.25° above the intersection of T_A with T_C for about 0.5 hour. Both T_H and T_C, after retaining their maxima for about 1.0 and 0.5 hour respectively, began a steady fall for about 20 hours, gradually approaching the T_A line. This demonstrates the typical reaction of the tree temperatures to a very rapid change in air temperature when not complicated by the presence of transpiring foliage or other disturbing factors such as occur when the tree temperatures cross the zero line. The true heat diffusion "lag" was about 0.5 hour for the cambium and 1 hour for the tree center. The maximum T_A, which held for about 2 hours just before the sudden drop, was 22.0° C. The number of "degree-hours" of atmospheric change was about 37, producing about a 10 degree-hour change in the tree center or a ratio of about 3.7 :1. This appears to be

TABLE XIII

INFLUENCE OF RISE IN AIR TEMPERATURE ON TREE TEMPERATURE WHEN NOT DISTURBED BY FREEZING OR THERMOSTASY

(1932) Jan.	T_A min.*	T_A max.	Diff. degrees	T_A min. hour	T_A max. hour	Diff. hours	T_H min.	T_H max.	Diff. degrees	T_H min. hour	T_H max. hour	Diff. hours	T_A rise / T_H rise
27	0.00	9.00	9.00	7:30 a. m.	2:30–3:30 p. m.	7	0.00	5.50	5.5	10:15 a. m.	8:30 p. m.	10.25	9.0 / 5.5
28	6.50	16.00	9.50	7:00 a. m.	2:30–3:30 p. m.	7.5	5.50	11.50	6.0	9:30 a. m.	7:30–9:00 p. m.	10	9.5 / 6.0
Cold Spell													
Feb. 7	2.25	13.00	10.75	9:00 a. m.	5:00–6:00 p. m.	8.5	2.00	7.50	5.5	1:00 p. m.	12:00–3:00 a. m.	11	10.75 / 5.5
8	Cold Spell												
9	2.00	19.00	17.0	6:45 a. m.	3:00–4:30 p. m.	8	1.50	11.50	10	10:30 a. m.	11:30 p. m.–12:30 a. m.	12.5	17.0 / 10.0
10†	19.75	28.50	8.75	7:45 a. m.	12:30–1:30 p. m.	5	15.00	22.50	7.5	7:45 a. m.	6:00–7:30 p. m.	10.5	8.75 / 7.50
Cold Spell													
13	5.75	13.00	7.25	8:30 a. m.	2:30–4:00 p. m.	8	5.50	9.00	3.5	10:30 a. m.	7– 8 p. m.	9	7.25‡ / 3.5
Cold Spell below 10° C.#													

22	1.25	8.25	7.00	9:30 a. m.	3:00–5:00 p. m.	6.5	1.25	6.00	4.75	10:30 a. m.	7:30–10:00 p. m.	9	7.00/4.75
23	1.00	6.00	5.00	11:15 a. m.	3:30–4:30 p. m.	4.5	1.00	3.00	2.00	2:00 p. m.	9:00–12:00 p. m.	7	5.00§/2.00
24	1.50¶	17.50	16.00	8:30 a. m.	2:30–5:00 p. m.	7	1.50	11.25	9.75	10:30 a. m.	9–11 p. m.	11	16.00/9.75
25	7.50	22.25	14.75	8:00 a. m.	3:30–6:00 p. m.	7.5	7.25	16.50	9.25	10:30 a. m.	10–11 p. m.	12	14.75/9.25
26	12.25	21.25	9.00	11:30 a. m.	4:45–5:45 p. m.	5.5	12.25	16.75	4.50	11:00 a. m.	8:30–10:00 p. m.	9.5	9.00/4.50
27	12.50	18.25	5.75	10:45 a. m.	2:45–5:00 p. m.	4	12.25	15.25	3.00	11:30 a. m.	8.:00–9:30 p. m.	8.5	5.75/3.00
28	10.50	22.00	11.50	9:30 a. m.	4:30–5:30 p. m.	7	10.50	16.50	6.00	11:30 a. m.	9:30–11:30 p. m.	10	11.50/6.00
29	12.50	18.50	6.00	11:30 a. m.	2:30–5:00 p. m.	3	12.00	15.25	3.25	1:00 p. m.	5–10 p. m.	5	6.00/3.25

* T_H min. and T_A min. hour taken at time of actual beginning of new daily rise of T_A or T_H, and at intersection of T_A and T_H, if any, and above 0° C.

T_A max. hour taken at time of first attainment of T_A max.

T_A max. and T_H max. taken as average of maxima covering more than one hour and at least 0.5° change, especially in T_H.

† A continuous rise day and night from 7 a. m., Feb. 9, to 12:30 p. m., Feb. 10, required estimates of T_A min. and T_H min. and hours on Feb. 10. Total ratio for this period T_A/T_H = 26.50/21.00.

‡ A rapid and severe drop in air temperature carried the air-temperature line across the tree-temperature line before the T_H max. was attained and hence reduced the T_H max. The T_H line began to drop 2 hours after this crossing and 4 hours after the T_A line began its drop.

On Feb. 18 a rise in air temperature from 0 to 5.5° C. caused a 3.0° rise in the tree, a ratio of T_A/T_H = 5.5/3.0.

§ Very short T_A max. which was well below 10° C.

¶ 1.5° C. was the point at which the air-temperature line crossed the tree-temperature line in its daily rise. Below this point the rise in air temperature could not cause a rise in tree temperature.

the usual approximate, maximum ratio when the disturbing factors noted above are absent.

Various other early-season records showing thermostasy have been previously cited, so that there is ample evidence of the presence of this phenomenon at various seasons and in different years.

Direct insolation of the tree accounted for a rise in the cambium during certain parts of the season. For example, on March 14, 1934, at about 9 a. m. the cambium temperature began to rise from 6 to 8° C., while the center temperature remained steadily at 5.5° C. and the air temperature remained below that of the cambium. A similar situation existed on the morning of March 18, when the cambium rose from 1.0 to 2.25° C., while the air temperature was from 1 to 2° below zero. On April 12, 13, 19, 20, 21, 24, and 25, direct insolation caused a rise of about 3.0° in the cambium temperature under circumstances similar to those of March 14 and 18, and with no evident corresponding rise in the center temperature. Several other examples are to be found in the records, as on February 26 and 27, 1932, and on January 31 and February 1, 1931, when the cambium remained approximately 2.5° higher than the atmosphere for from 3 to 4 hours.

The direct effect of air temperature upon the tree temperature is well shown in table XIII under the column T_A rise/T_H rise. It is evident from these data that since the ratio never reached 3:1, less than 3° of air-temperature rise was needed to cause a rise of 1° in the tree center. This period of the year was of course free from the complication of thermostatic cooling or other effects due to the presence of foliage and its transpiration. It will be noted that this rule held at all temperatures above 0° C. and when the minimum air temperature was at or above that of the tree. When the air temperature was below that of the tree it of course could not raise the tree temperature, and in preparing the table all air temperatures below the minimum tree temperatures were ignored. Any heat derived from direct insolation of the tree trunk at the thermometer level would tend to increase the factor "T_H rise" and thus lower the

ratio. That this possible disturbing factor probably did not seriously alter the ratio is indicated by a comparison of the ratios in table XIII with those between the temperature drop of the air and of the tree at night during this same period, as seen in table XIV. The average ratio during the day was about 1.71 :1 and during the night about 1.64 :1.

Discussion and Conclusions

LAG

In former publications the word "lag" has been used to cover any departure in time between an air temperature and a supposed correlative tree temperature. Most frequently it has been used to cover the period between an air-temperature maximum or minimum and the following tree-temperature maximum or minimum respectively, on the assumptions, first, that the transfer of heat into or out of a tree requires time, and second, that the tree-temperature maximum or minimum is directly and only due to the preceding air-temperature maximum or minimum more or less modified by factors of relatively slight importance. The first of these assumptions is of course correct, but many authors have also tacitly assumed that the time consumed in the transfer of heat would vary from time to time in the same tree as well as in different trees. The second assumption, as has been demonstrated in this investigation, will have to be fundamentally and seriously modified, although it is clear that the air-temperature changes under certain conditions are reflected directly, in modified form, in the changes in the tree temperatures.

An examination of the records as already presented demonstrates that the rate of conduction of heat across the tissues is for an individual at a given place a constant, which under the given conditions may be stated as follows: A readily detectable change of temperature at the cambium layer occurred in less than 0.25 hour and in the tree center in less than 1.5 hours. For purposes of this paper these periods of time have been called the "true lag" periods. Theoretically a change of temperature

TABLE XIV

INFLUENCE OF REDUCTION OF AIR TEMPERATURE ON TREE TEMPERATURE

(1932) Feb.	T_A max.	T_A min.	T_A loss*	T_H max.	T_H min.	T_H loss	Ratio $\frac{T_A \text{ loss}}{T_H \text{ loss}}$
7–8	7.50	0.00	7.5	7.5	4.5	3.00	$\frac{7.5}{3.0}$
12–13	17.75	2.00	15.75	17.75	5.5	12.25	$\frac{15.75}{12.25}$
13–14	13.00	5.25	7.75	9.00	1.0	8.00	$\frac{7.75}{8.00}$
19–20	5.00	–3.00	8.00	5.00	–1.00	6.00	$\frac{8.00}{6.00}$
22–23	5.00	–1.5	6.5	5.00	1.00	4.00	$\frac{6.50}{4.00}$
24–25	11.00	4.00	7.0	11.00	7.25	3.75	$\frac{7.00}{3.75}$
25–26	16.00	8.5	7.50	16.00	12.25	3.75	$\frac{7.50}{3.75}$
26–27	16.25	9.00	7.25	16.75	12.25	4.50	$\frac{7.25}{4.50}$
27–28	15.50	6.00	9.50	15.50	10.50	5.00	$\frac{9.50}{5.00}$
28–29	16.50	7.00	9.50	16.50	12.00	4.50	$\frac{9.50}{4.50}$
29–3/1	15.25	9.00	6.25	15.25	10.50	4.75	$\frac{6.25}{4.75}$

* The decrease in air temperature (T_A loss) was taken between the point of intersection of the air-temperature line with the tree-temperature line (the T_A max.), and the point of actual minimum air temperature (T_A min.).

at the surface of the tree would be propagated through the tissue at a very high rate, of the order of the propagation of any other true wave in elastic matter, and in general determined by the thermal conductivity of the tissue. Since the detection of the change would depend upon the relative delicacy of the thermometer and since the limit of the instrument used here was about 0.25° C., in order to record a temperature rise, enough heat must have accumulated at the point of its insertion to cause .25° of temperature change. The average density and specific heat of the system would be the main factors determin-

ing the time consumed before enough heat had accumulated to cause this change. The rate of this accumulation of heat in the tissue is dependent upon the amount and rate of change in the air temperature and the *diffusivity* of the system, designated by the symbol ''h^2'' which equals K/CP, where ''K'' is the constant of thermal conductivity, ''C'' is the specific heat, and ''P'' the density (Ingersoll & Zobel, '13). The ''true lag,'' as used in this paper, is therefore essentially invariable, at least within the medium temperature limits and the usual liquid water content of the tissues. In many of the older papers on this subject, however, the ''lag'' periods reported were extremely variable and irregular from day to day and over longer stretches of time. This was due partly to the method of determining the ''lag,'' and partly to the unrecognized thermostatic factors.

It has already been noted that the intersection points of the air-temperature line with the tree-temperature lines are most important in the temperature curves, since they indicate usually momentary identical temperatures. These intersection points, which are here called *iso-thermal nodes,* have seldom been noted heretofore in the numerical data of this subject, and their significance has therefore been overlooked. It will be evident from an examination of the various temperature graphs during medium temperatures that the period from the air-temperature maximum to the following iso-thermal node was very irregular. This was influenced, first, by the rate of rise of the air temperature to the maximum, which therefore affected the rate of rise in the tree temperatures. Second, the length of the maximum period also influenced the rate and length of the rise in the tree temperatures, as well as helping to determine directly the length of time from the air maximum to the intersection. Since in most former records the length of this maximum period was undetermined, its effect on ''lag'' was entirely ignored. Third, the rate of decline in the air temperature prior to the intersection greatly influenced the apparent ''lag'' period. In general, a slow decline postponed the time of intersection of the lines, sometimes by many hours, and

a rapid decline greatly shortened this time. Now, since the maximum tree temperatures must occur *at* or *after* the intersections it is evident that the "apparent lag" between air and tree maxima must be an extremely variable quantity. Fourth, the rate of decline in the air temperature subsequent to the intersection caused variations in the length of time between the intersection and the maximum in the tree temperatures. This was influenced largely by the diffusivity of the tissues, since loss of heat by the tree could now take place in proportion to the speed of decline in the air temperature.

Analogous considerations demonstrate that the "apparent lag" between the air and tree minima also is necessarily very irregular. It has been unexplained in former investigations, due largely to incomplete data and a lack of recognition of the iso-thermal nodes. The two other factors, however, which in even greater measure and in a more important manner influence the lengths of "apparent lag," are: first, the adjustment period at the zero line, and, second, the thermostatic cooling of the tissues.

In most of the periods of declining air temperature in which the tree temperatures fell below 0° C., the tree-temperature minima were delayed by the long zero-adjustment period until many hours after the beginning of the air minima. In a few cases, notably that of January 28, 1934, a rapid decline in air temperature carried the tree temperatures below the zero line, and the tree minima were delayed due to adjustments gradually made while the tree temperatures were dropping. In a similar fashion, the tree temperature maxima, following a rise in air temperature which carried the tree temperatures above zero, were usually attained many hours after the air maximum, and in many instances the air temperature had several maxima and minima which were not even registered in the tree temperatures. This delay and frequent lack of registering of maxima were associated with the long zero-adjustment period which greatly modified the usual somewhat rhythmic rise and fall in the tree temperatures associated with the usual daily rhythm of air temperatures.

The effect of the thermostatic cooling upon lag was shown in the extreme form in July, 1934, when the low tree temperatures and the high air temperatures usually exactly coincided (and vice versa). The apparent rhythmic lag of approximately 12 hours was then entirely false, since the tree minima and maxima had no relationship to the preceding air minima and maxima respectively, as demonstrated in a former section of this paper. In less extreme cases, as during the latter part of July, 1930, the minimum period in the tree center partly coincided with the air-temperature maximum and vice versa. This condition in part obliterated the ''apparent lag'' period by substituting more or less of the false ''apparent lag''; in other words, the tree minima, due to preceding air minima, merged more or less completely with the minima due to the thermostatic cooling action. Likewise, the preceding air maxima caused a rise in the tree temperature which merged with the rise associated with the decreasing thermostatic cooling action, and the apparent lag period was somewhat extended.[1]

FACTORS AFFECTING TREE TEMPERATURES

As was early recognized by plant physiologists, the atmosphere and direct insolation are the main sources of heat for the plant. Many attempts were made in the early days of the subject to demonstrate elevated temperatures of the embryonic regions of the stem associated with respirational activity, but few satisfactory results were obtained because of the masking effect of the rapid and excessive changes due to the outside environment. In the course of these investigations experimenters became greatly impressed with the rhythmic alternations of temperatures in the tree, apparently following more or less regularly those of the air. Many of the investigators recorded considerable deviations of the tree temperatures from those of the air, but were usually content to point out that the mean temperatures of the tree and of the air ran parallel. From the present records the importance of the air temperature as the main factor in determining directly and also indirectly the tree

[1] Another type of ''false apparent lag'' has been described in a preceding section.

temperature is evident. However, the factors influencing the diffusion of heat through the tissues, which is a basic physical phenomenon, must be clearly defined in order to interpret the various reactions indicated in the graph-records.

The order of magnitude of the thermal conductivity of wood is indicated by that of pine, which at 15° C. and perpendicular to the face is given as $0.361\ \lambda \times 10^{-3}$, while that of water at 12° C. is $1.36\ \lambda \times 10^{-3}$.[1] Hence the heat conductivity of the tree trunk would tend to increase or decrease (directly) with an increasing or decreasing proportion of water. As indicated later, concurrent with a decreasing water content there is an increasing amount of water vapor, and since its thermal conductivity is less than that of water (e.g. at 46° C., $4.58\ \lambda \times 10^{-5}$) the rate of heat transfer in the entire system would be further reduced by this factor. Under the high transpiration conditions of the summer the center temperature tended to respond less readily to changes in air temperature than under more moderate conditions. In light of the above, this may be partly accounted for by a net loss of water from the tissues, resulting in a decrease in heat conductivity. That there is a tendency toward a decreasing water content of trees as the transpiration rate increases has been demonstrated by various investigators (MacDougal, Overton & Smith, '29), and a study of the various patterns of water distribution in tree trunks at different seasons points toward the general conclusion that there are sharp differences in seasonal distribution and quantities of water in tree trunks (Craib, '18–'23).

Since the specific heat of ice at –10° C. is approximately half that of water at 0° C. (0.48 vs. 1.0087) the reactions of the tree temperatures to subfreezing air temperatures would tend to be more rapid when the water in the tissue is frozen than when liquid. Moreover, the heat conductivity of ice is more than quadruple that of water, or about $5.7\ \lambda \times 10^{-3}$. This physical factor also would tend to increase the speed of reaction of tree temperatures to low air temperatures as compared with the reaction at temperatures above zero. While it is not possible

[1] Physical data from Lange ('37).

at present to determine from the records the relative quantitative effects of these factors they must be considered in any attempt at a complete analysis of the factors concerned. In general, it has already been shown that the ratio between the increase or decrease in atmospheric heat and the increase or decrease in the center temperature is higher at higher temperatures and lower at lower temperatures. This must be ascribed mainly to the thermostatic cooling at higher temperatures. However, these heat-transmission factors under extreme conditions may be sufficiently important to affect noticeably the general result, as would be indicated by the fact that when the tree was at sub-zero temperatures the ratio air-temperature change/tree-temperature change was unusually low, even reaching the theoretical ratio of 1:1 as cited elsewhere. This contrasts somewhat sharply with the usual ratio at temperatures above zero when there was little thermostatic cooling, and indicates less heat absorption and more rapid heat transmission at sub-zero than at supra-zero temperatures. During the winter sub-zero periods the tree-temperature lines were more often superimposed and also more closely followed the air-temperature line in its wanderings than during early spring and late fall supra-zero periods. This general observation may be explained mainly by the recognition of these physical factors.

In a consideration of the phenomena which have been heretofore included in the phrase "zero-line adjustment," it is clear that at or just below zero, because of the latent heat of fusion of ice, heat is steadily given off as ice formation proceeds. The steady temperature at or near the zero line is thus maintained until ice formation is complete, and a continuance of an air temperature below that of the tree would cause a lowering of the tree temperature. The reverse process would take place during the crossing of the zero line concurrent with the rise of temperature. The following data seem to substantiate this concept. During the period, January 29–February 6, 1932, the center temperature line held at about –1.5° C. almost steadily, although the air temperature line was above zero for

3 days or more. However, the number of degree-hours below zero during the first cold spell was about 327, while during this first warm spell, which did not carry the temperature of the tree center above zero, it was only about 244. That this use of degree-hour units is a valid criterion is evidenced by the fact that for the entire period the total degree-hours below zero (421) just about equaled the number above zero (432), the period beginning at the time that the center temperature line crossed the zero line on its way down and ending when it recrossed the zero line.

The relatively long period during which the temperature of the tree hangs at about 0° C., even when the outside temperature is steadily dropping, may possibly be associated with the phenomenon of change of "free water" to "bound water." Newton and Gortner ('22) show that winter hardy wheat changes its free- and bound-water relationship at low temperatures, and such changes may well occur during this transition period in the tree. Gortner ('37) states that "by bound water we mean water molecules which have been so reduced in activity that they are not oriented into the crystal lattice pattern, characteristic of ice, when exposed to low temperature," and he evidently considers the binding of water as an adsorption process (Gortner, '38) which, as is well known, evolves large quantities of heat. It may then be possible that more or less of the heat evidently evolved in this "adjustment" period is derived from this source. Moreover, it has already been shown that even when the air temperature declines so rapidly that the tree temperatures are carried past the zero point an evolution of heat can still be demonstrated, proving that the adjustment process still takes place. Whether or not super-cooling occurs under these circumstances cannot yet be definitely proven, but it is entirely possible. Since this phenomenon is facilitated by the absence of active liquid movement (Luyet & Hadapp, '38) and the whole mass of water in a tree trunk is divided by the cell walls and membranes into numerous partially immobilized small units, the conditions for super-cooling would be especially favorable. The influence of the higher

osmotic concentration of the biological fluids on the freezing point during the zero-adjustment period is shown by the fact that the temperature during this time was from –0.50 to –1.50° C. instead of 0° C., with the lower temperature predominating when the temperature was on the decline.

SOIL TEMPERATURE

Several investigators have maintained the hypothesis that the temperature of the ascending soil water caused tree temperatures above or below those of the air. It was pointed out that if the transpiration stream had a different temperature from that of the air it would tend to modify the effect of the air temperature by constantly giving off or taking up heat. In some cases soil temperatures were correlated with tree temperature in substantiation of the hypothesis. Hartig ('73), in his table II, shows that a cut, living log containing water accumulated heat in the direct sunlight, while a standing transpiring tree (oak) under similar conditions, even at 4 cm. deep, definitely cooled not only to a temperature below that of the cut log but also in general below the air temperature. The cooling action could be seen in a shaded location also, although it was not so great. The cumulative heating of the log in the sun was marked, especially at the 4 cm. depth. Selected data are given in table XV.

TABLE XV

DATA ASSEMBLED FROM TH. HARTIG

Time	Outside sun temp. rise or loss	Log temp. rise or loss	Tree temp. rise or loss
6–8 a. m.	+8.2° C.	+3.8° C.	–0.3° C.
8–10 a. m.	+12.3° C.	+6.2° C.	+1.7° C.
10–12 a. m.	+0.4° C.	+6.5° C.	+1.3° C.
12–2 p. m.	+1.6° C.	+2.3° C.	+1.2° C.
2–4 p. m.	+1.0° C.	+2.0° C.	+1.5° C.
4–6 p. m.	–2.6° C.	–2.3° C.	+1.0° C.
6–8 p. m.	–5.8° C.	–4.0° C.	+1.0° C.

The air temperature (in shade) also showed a decline from 4 to 6 and 6 to 8 p. m.

Several items of interest appear in this table: (1) The manifest cooling action in the transpiring tree which held the temperature rise to less than 8° C. as contrasted with rise in the log temperature of nearly 21° C; (2) the slower rise in the log temperature as compared with that of the outside, probably because of the high specific heat of water; (3) the continued rise of temperature in the tree due to the fact that the outside temperature, although declining, was still above that of the tree and contributing heat to it; (4) the rise in temperature and accumulation of heat in the water-containing, but essentially non-transpiring log. This independent demonstration of cooling action, ascribed by Hartig to cool soil water, is of special interest, since the data were gathered from a study of a different species growing under different climatic conditions. If in the present study the cooler temperature in the tree had been due to cool water ascending from the lower cool regions of the soil, there should be specific evidence in the records. Cool water, at its maximum speed of flow, passing through the stem for one or more hours, should have somewhat reduced the tree temperature during the extended periods of maximum air temperature. However, at no time is there evidence that this took place. Moreover, there is no evidence that during the night a cooling of the tree tissues occurred due to cool water from the ground, since usually when the air temperature was at its minimum, the maximum center temperature had been reached and maintained. The only possible evidence in favor of the cooling action of soil water is that early in the morning, before the sharp rise in air temperature, the center temperature sometimes made a slight drop before the sharper drop of the day. However, this can be explained by the same factors that account for the major cooling action as discussed later.

Furthermore, the cooling effects reported here could not be considered as due to the temperature of the soil water for the following four reasons: First, the greatest cooling was in the center where, it is universally agreed, there is the least conduction of water and where gases predominate. Second, when the temperature of the air began to drop that of the center be-

gan to rise, while that of the cambium usually accelerated its rise. This change of tree-center temperature could hardly be ascribed to a change of temperature in the soil water, nor to its warming-up due to slower conduction, since the center was affected as soon as the conducting region. Third, the amount of change in the cambium temperature was somewhat proportional to that of air temperature and less than that of the tree center, whereas it should have been more if due to a change in the temperature of the transpiration stream. Fourth, the beginnings of these responses were essentially instantaneous, which could not have been true if they had been dependent upon the rise of the water from the soil through 30 to 40 feet of vascular tissue. Finally, the marked cooling action during July, 1934, could not have been associated with the passage of cool soil water through the trunk, as evidenced by a comparison of the records of corresponding dates of other years. When, for example, as shown by the continuous chart record during much of July and early August, 1932, the air temperature varied slightly, the temperatures of the cambium and of the center varied mainly between 25 and 30° C. In July, 1934, during the prolonged hot period the tree minima were often close to 15° C. Manifestly, the soil temperature in the same location could not have been approximately 15° C. in 1934, and 25° C. in the cooler year of 1932. While there is thus no evidence that the temperature of the soil water is the main factor in controlling the temperature of the tree, it seems probable that it is a contributing factor in modifying the final temperature.

The same general statement applies, in some degree, to the belief that the warmer soil temperature of winter might be a source of heat which flows upward through the root system into the tree trunk, thus helping to maintain a temperature in the tree trunk somewhat higher than that of its surroundings. Such a hypothesis has no basis in direct observation.

STRETCHING OF WATER COLUMNS AND VAPORIZATION

The presence of water vapor in the tissues of the tree has long been taken for granted, and Scheit and von Höhnel, by

various ingenious experiments, demonstrated the probability of water vapor in the tracheae. Nevertheless the corollary of this concept, namely, that by the absorption of heat in the process of vaporization the tissues would necessarily be cooled, has apparently not been given due consideration. There has been much discussion concerning the presence or absence of air bubbles in intact tracheae of the hydrostatic system, but at least a certain amount of water vapor would necessarily be present in such bubbles. The amount of vaporization into these bubbles would increase with an increasing negative pressure, resulting in an increased absorption of heat from the surrounding tissues. Vaporization into the pneumatic system would likewise cool the tissues. If, as is postulated in the traction-cohesion theory of water transfer, the water columns become stretched and if this liquid acts similarly to other substances under stress, it would be cooled in accord with the well-known physical principle that substances which expand upon heating absorb heat in the process of stretching. Thus two possible physical processes exist which seem to fulfill the general known or postulated conditions in the tree and which separately or together may account for the cooling action demonstrated in these studies. A careful consideration of the detailed records and of the various special conditions involved should give some indications whether one or the other of these physical processes is to be given preference in the formulation of a theory.

The general considerations involving the relationships between the several factors under study here have been given in considerable detail by MacDougal, Overton and Smith ('29). Certain of their conclusions which have important bearings upon this problem are given here.

"A cohesive meshwork of sap occupying portions of all untylosed annual layers of these trees.

"The cohesive columns of water occupying the tracheids and vessels are in a state of tension set up by evaporation from the exposed walls of cells adjoining intercellular spaces of leaves.

"Dendrographic studies made show that the pull set up by water-loss from such surfaces causes daily variations in size of intact stems and trunks, owing to an increase and decrease of the tension.

"Pressures and suctions on the gaseous system within the trunk are readily transmitted vertically for distances many times the length of the vessels. Tangential transmission of suctions and pressures is at a very slow rate, and is even slower in a radial direction.

"The relative volumes of the hydrostatic and pneumatic systems within the tree are subject to variation during the course of the season. Specific conducting elements may at one time be partially or wholly filled with gas, and at another time filled with water.

"Tensions in the pneumatic system may vary from something less than half an atmosphere to not more than one or two atmospheres. Tensions of the hydrostatic system may vary from a compression or positive pressure to a suction or pull of one to two hundred atmospheres."

It would appear then from the studies of MacDougal and his associates that the increased foliar transpiration under increasing air temperature might produce two effects as related to this problem. The greatly increased tension of those water columns which remained intact would cause absorption of heat from the surrounding tissues. Moreover, vessels might be added to the pneumatic system by the breaking of their water columns, associated with an increased production of water vapor, and the extraction of heat would effect an increased cooling in the tissues. This condition of greatly stressed water columns seems to require that the greater cooling action should be at the place of greatest tension, which would be in the younger wood near the cambium zone. However, in these studies the colder area was always found to be in the tree center, whenever thermostatic conditions could be demonstrated. There seems to be no combination of circumstances in the tree trunk by which the greater cooling action could take place at an outer layer of tissue and cause a lower temperature in an inner region. Although we cannot ascribe the main cooling of the tree center directly to the stretching of water columns, at the cambium layer this might be an important, or even the major, cause. Since the cambium layer would receive much more heat than the center by conduction from the outside, it is probable that there would be a considerably greater potential cooling force there than is evident by the temperature recorded. If, on the other hand, we assume with Priestley ('32) that there is no such great tension on water columns, then

vaporization of water in the tissues appears to be the only adequate physical principle to account for the notable cooling action with its immediate response to changes in air temperature.

As this discussion indicates, the conditions necessarily postulated under either hypothesis would lead to some vaporization. This process absorbs a large amount of heat (584.9 gram-calories per gram at 20° C. to 574.0 at 40° C.) from the immediate environment and cools it proportionately. The inner tissues of the tree, being somewhat insulated from the surrounding atmosphere, may attain and for some time may hold in part a temperature considerably different from that of the environment. Any conversion of water to water vapor will thus tend to cool the tissues in proportion to the amount vaporized. An advancing air temperature would usually induce a higher rate of foliar transpiration which in turn would cause a greater rate of internal vaporization. With a drop in air temperature the rate of transpiration, and with it the rate of internal vaporization, would decrease. This would result in a decrease in the cooling of the tissues and a consequent rise in temperature, due to the flow of atmospheric heat inward and possibly to a positive release of heat in the tissues through the transformation of water vapor to water.

Since there is a steady flow of heat into the tree, there must be a steady absorption of this heat, as was demonstrated by the fact that the tree temperature does not rise and may even become lower. This would mean, under the vaporization hypothesis, that vaporization must be maintained concurrently with this inward flow of heat. Since increasing transpiration leads to water deficit in the tissues, including the stem, increased space is constantly being made available for water vapor, more or less in direct proportion to the rate of transpiration. Vaporization would tend to continue until an equilibrium has been attained, but due to the changes in rates of transpiration it would not for long remain poised. It is assumed that the walls of the tracheae in the hydrostatic system are constantly moist and that whenever they are in contact with spaces in the pneumatic system vaporization proceeds as indicated above. More-

over, throughout the pneumatic system there would be a tendency for the vapor pressures to become equalized. The movement of vapor longitudinally would doubtless be very rapid, as MacDougal and his associates ('29) have demonstrated that pressures are transmitted longitudinally at relatively high rates. Imbibition in the walls and diffusion of vapor through the lumina would account for the lateral equalization. The relationships of water and water vapor to each other and to the structural units seem to provide an adequate system in which vaporization would be effective in the tree trunk. However, the question of the relationship between the foliar transpiration and vaporization in the vascular region is important. It is generally accepted in the traction-cohesion theory that transpiration causes a definite pull upon the water in the vascular elements of the leaf which is transmitted downward through the connecting vascular elements to the entire body of water in the hydrostatic system. Apparently the tendency toward rarefaction of the pneumatic system which would be induced by the tension on the hydrostatic system is partly compensated, since MacDougal and associates ('29) did not find negative pressures in the pneumatic system corresponding with those possible in the hydrostatic system. It would seem probable, in view of the sharp cooling at the tree center, that at least some, if not all, of this compensation is associated with the added production of water vapor. This might account also for the almost instantaneous inverse response of the center temperature to increase in the air temperature. On the other hand, Priestley ('32) accepts the concept of the presence of water vapor in some elements essentially throughout the vascular system, with the water columns breaking and vapor replacing the water in additional tracheae as transpiration increases. This replacing of water by vapor would cause the cooling of the tissues. Priestley's concept also definitely implies a partial rarefaction of the contents of the tracheae, which might extend rapidly for long distances throughout the vascular system until a temporary equilibrium had again become established. Hence this concept also might account for the almost instantaneous nature

of the temperature responses. The greater cooling at the tree center may be associated with a reduction in the water content there, thus leaving more space for vaporization from the inner front of the hydrostatic system.

The effect of temperature upon the water-vapor holding capacity of air is an important factor in the internal adjustments of the tree. The mass of water vapor in saturated air at 10°, 20°, and 30° C. is given as 9.398, 17.28, and 30.36 grams per cubic meter respectively, or, an increase of over 83 per cent between 10 and 20° C., and of over 75 per cent between 20 and 30° C. Hence, concurrent with a rise in temperature within the tree, in response to a rise in the environmental temperature, there would be an increase of the water-vapor capacity of the pneumatic system. This in itself would cause an increased vaporization with a corresponding abstracting of heat, thus preventing the full potential direct response of the tree temperature to changes in the environmental temperature. It would also provide for a more effective increase in internal vaporization associated with increased foliar transpiration. On the other hand, coincident with a decline in the internal tree temperature, there would be a decreased vapor capacity in the pneumatic tissue resulting in a condensation of water vapor to water with its attendant release of heat to the tissues and therefore a decrease in the cooling action. This may account largely for the fact that even when the tree was bare of foliage and the air temperature rose sharply, as from 10 to 20° C., the tree center failed to respond as rapidly or to attain as high a temperature as the air. This phenomenon is well shown in the records for February 24 and 25, and March 18 and 19, 1932, as well as in many other similar periods of the year.

The data given in this paper demonstrate an almost instantaneous influence of the air temperature upon the cooling action in the stem. The anatomical structure of the stem system in general provides an excellent channel through which such a rapid action could take place. The veins of the leaf, through the petioles and twigs, connect downward with the cone of vascular tissue of the older stems. In passing from the lower por-

tion of the stem upward the older layers of wood, one at a time, "run out," but sheathed by and connected with the younger layers. Since the foliage system as a whole is connected with all of the layers of both the hydrostatic and the pneumatic systems, its influence can reach every portion of the vascular system which is not blockaded against the fluid contents of the tubular elements. Whether we conceive of the transpirational pull acting upon the liquid contents of the hydrostatic system or upon the gaseous contents of the pneumatic system, we have an adequate channel through which this pull may act very rapidly and affect more or less every portion of the vascular tissue. As required by the data in this paper, an increased transpirational pull, induced by increased air temperature, will be transmitted rapidly through the water of the hydrostatic system to places where this system and the pneumatic system come in contact. There the water will tend to retreat into the tracheae, thus tending to increase the air space. Because this reduces the vapor tension in the air space instantaneous vaporization into the pneumatic system will take place, the amount depending directly upon the strength of the transpirational pull. It seems probable then that a considerable amount of the cooling action in the tree is associated with internal vaporization into the pneumatic system. In addition there may be a certain amount of cooling in the hydrostatic system, associated with and in direct proportion to the amount of stretching of the water columns. This physical action might under some circumstances cause the major portion of the heat absorption from the tissues of the hydrostatic system, depending upon the ability of the system to develop a continually increasing amount of stress. If the water were immobilized in the tracheae, or the transpirational pull ceased to increase and the system were then at rest, so far as additional force is concerned, there would then be no additional cooling and the temperature would begin to rise due to the inward flow of heat. This latter condition would perhaps be the main reason that the temperature of the cambium tended to rise earlier in the day than did that of the center, when the air temperature approached and held its maximum.

A second question in connection with the thermostatic action is why the cold temperature of the tree is maintained for a time and then, in immediate response to the beginning of the decline in the air temperature, begins to rise. Because of the high specific heat of water and its low thermal conductivity the layer of hydrostatic tissue acts as an excellent insulation, preventing the rapid inflow of heat to the inner tissues. This, together with such positive cooling as may take place in the hydrostatic system, would tend to hold the low temperature of the interior. When, however, the air temperature begins to drop, the transpirational pull decreases, the stressed hydrostatic system tends to reoccupy some of the pneumatic area, and vapor changes back to water, thus releasing heat. It appears then that all of the major questions associated with the thermostatic action are answered on the basis of the hypothesis discussed above.

At different times of the year and under different climatic conditions these various modifying factors differ in their influence on the tree temperatures and on the form of the curves, so that it is difficult to draw definite conclusions as to their importance except in certain of the more obvious cases. Broadly speaking, the temperature of the environment is the major factor determining the tree temperature. Certainly the major modifying influence around the zero point is the physical and physiological adjustment which takes place, while at sub-zero temperatures the tree temperatures closely follow those of the air. Under conditions of high transpiration, especially when due to high temperatures, the thermostatic cooling is the main modifying factor, and this may at times nearly cancel the effect of increasing air temperatures. During moderate temperatures thermostatic action is more or less manifest as a modifying factor, especially during the period of completely developed foliage. Throughout all of the year the form of the curve is greatly influenced by the speed of air temperature change and the lengths of the maximum and minimum air-temperature periods. It is especially important, in attempting to explain the apparent temperature responses in the tree, to locate the iso-thermal nodes and to determine the conditions before and after these points.

From time to time during the last hundred years the subject of water vapor in the vascular system of plants has been discussed in botanical contributions. The accurate, refined temperature-recording apparatus used in this study, combined with other appropriate studies, should develop important information toward an understanding of water-vapor in relation to the hydrostatic system and of its significance in water transport.

From the data presented in this paper it seems evident that the severity of temperature extremes and of temperature changes may be considerably mitigated for the plant through the zero-adjustment period and the thermostatic action. Much higher temperatures in the plant tissues certainly would occur were it not for the latter, and it may be significant that whereas temperatures capable of injuring protoplasm might readily develop from direct insolation, injury of this type seldom occurs under active transpiring conditions. In this investigation cambium temperatures were held well below 40° C., although even the shade temperatures on some of these days continued above 42° C. for several hours. At the other temperature extreme, the injurious effects of the freezing and thawing may perhaps be somewhat reduced by the long period over which the uniform temperature close to the freezing point is usually maintained.

Summary

1. Former studies of tree temperatures were inadequate because of lack of proper apparatus and of continuous observation.

2. A continuous, accurate, detailed, automatic record of air temperatures and cambium and center temperatures of a cottonwood tree was kept for about four years.

3. A typical record for one day is described; special precautions which are necessary in interpreting the records are cited; and the "degree-hour" is described.

4. A summary of certain general results shows that at about the zero point the tree temperatures usually do not follow immediately that of the air, and often do not drop below zero until

after 24 or more hours, whereas below zero as a rule they closely approximate the air temperature; at high temperatures there is a thermostatic cooling action in the tree tissue which partly or entirely counteracts the effect of the flow of heat inward; in extreme cases a temperature at about 15° C. was maintained when the air temperature was about 42° C., and the cambium was intermediate; high foliar transpiration producing a water deficit in the vascular tissues is indicated as inducing internal vaporization and consequent cooling of the center; at medium air temperatures the tree temperatures followed them, but considerably modified by thermostatic cooling and other factors.

5. A detailed examination of a number of "case studies" during the low temperature periods demonstrated that the temperature of the center has a distinctly modifying effect on that of the cambium; that after the zero-adjustment period the "lag" was for the cambium about 0.50 hour and for the center about 1.5 hours; that during the zero-adjustment period the ratio air-temperature change/tree-temperature change was high and in sub-zero weather low, even attaining the theoretical value of 1:1; that even when a rapid drop in the air temperature carried the tree temperatures across the zero-line with little "apparent lag" the internal adjustment can be demonstrated by a study of this ratio.

6. "Case studies" of high-temperature periods demonstrated that the thermostatic cooling of the tree tissues was a universal phenomenon; that this was essentially an instantaneous response to changes in air temperatures; that the cambium was kept at a lowered temperature by this action; that the tree temperature was a resultant of the flow of heat inward and of the thermostatic cooling; that from July 13 to 26, 1934, the exceptional uniform conditions produced approximately a "controlled experiment" for the study of the effects of air temperature upon those of the tree; a modified "degree-hour" method was useful in estimating these effects; that "true lag," which is the measure of the rate of flow of heat across tissues, can be distinguished from "apparent lag," which is a composite of

many factors; that "apparent lag" was essentially eliminated by the thermostatic action during this exceptional high temperature period; that direct insolation was a minor factor at this season of the year; that the "true lag" in the cambium was 0.50 hour and in the center 1.50 hours or less.

7. The main conclusions from the selected "case studies" during the medium temperature periods were that thermostatic cooling was effective in various years and essentially from the beginning of the period of full foliage, thus indicating that transpiration is the means by which air temperatures affect thermostatic cooling; that the "true lag" periods were here usually the same as for high- and low-temperature periods; that direct insolation was a factor in the cambium temperature at times but at most a minor factor which could not be clearly detected in the center temperature.

8. The problem of "lag" throughout the records is discussed. It is shown that the intersection points of the air-temperature line with the tree-temperature lines, which are denominated "iso-thermal nodes," are important in analyzing the records and in determining the reasons for the "apparent lag" of the tree temperatures behind the air temperatures. The "lag" periods of older writers were of very irregular length due in part to incomplete records and in part to an apparent misconception of the factors affecting lag.

9. While the air temperature is the major factor in determining the broad limits of tree temperatures, its effect is greatly modified by various factors, some of which were discussed in preceding sections. In addition to those, the following are considered: the thermal conductivity of wood substance and of water and of water vapor; the different specific heats of water and of ice; the latent heat of fusion of ice; "free" and "bound" water; and the osmotic composition of the cell sap. The temperature of the soil water apparently had little effect in determining these tree temperatures, and it is doubtful if it is ever an important factor. This conclusion applies also to the flow of heat from the soil through the tree tissues.

10. The stretching of water columns and vaporization within

the tissues, both due mainly to foliar transpiration, are suggested as the main, more or less cooperating, causes of thermostatic cooling. These are considered both in light of the factual physiological and anatomical evidences and of various theories. In general, it appears that stressing of water columns may be important in the young wood layers near the cambium; and the vaporization process especially important throughout the pneumatic system, whether permanent or temporary. The difference in the vapor capacity of the air of the pneumatic tissue, due to differences of temperature, causes a direct thermostatic action, as well as having a modifying effect when the transpiration rate is changing. The hypothesis suggested is believed to be adequate and no other at present seems to fit the known facts.

11. Some suggestions are made as to the possible relative importance of the main factors in influencing tree temperatures; the special value of this method of investigation as applied to certain other important problems in tree physiology; and the possible protective benefits which the plant may derive from the temperature adjustments studied in this paper.

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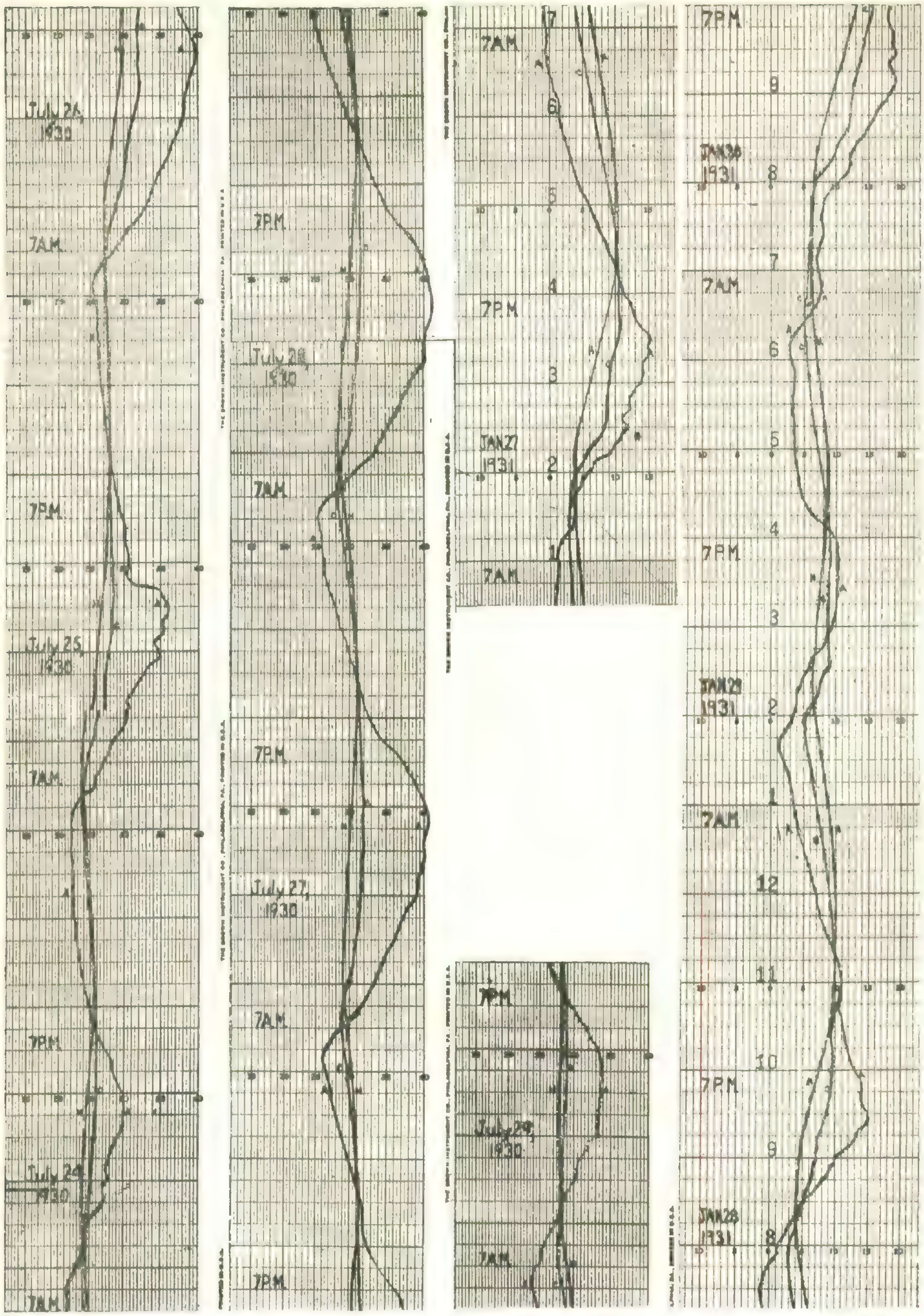

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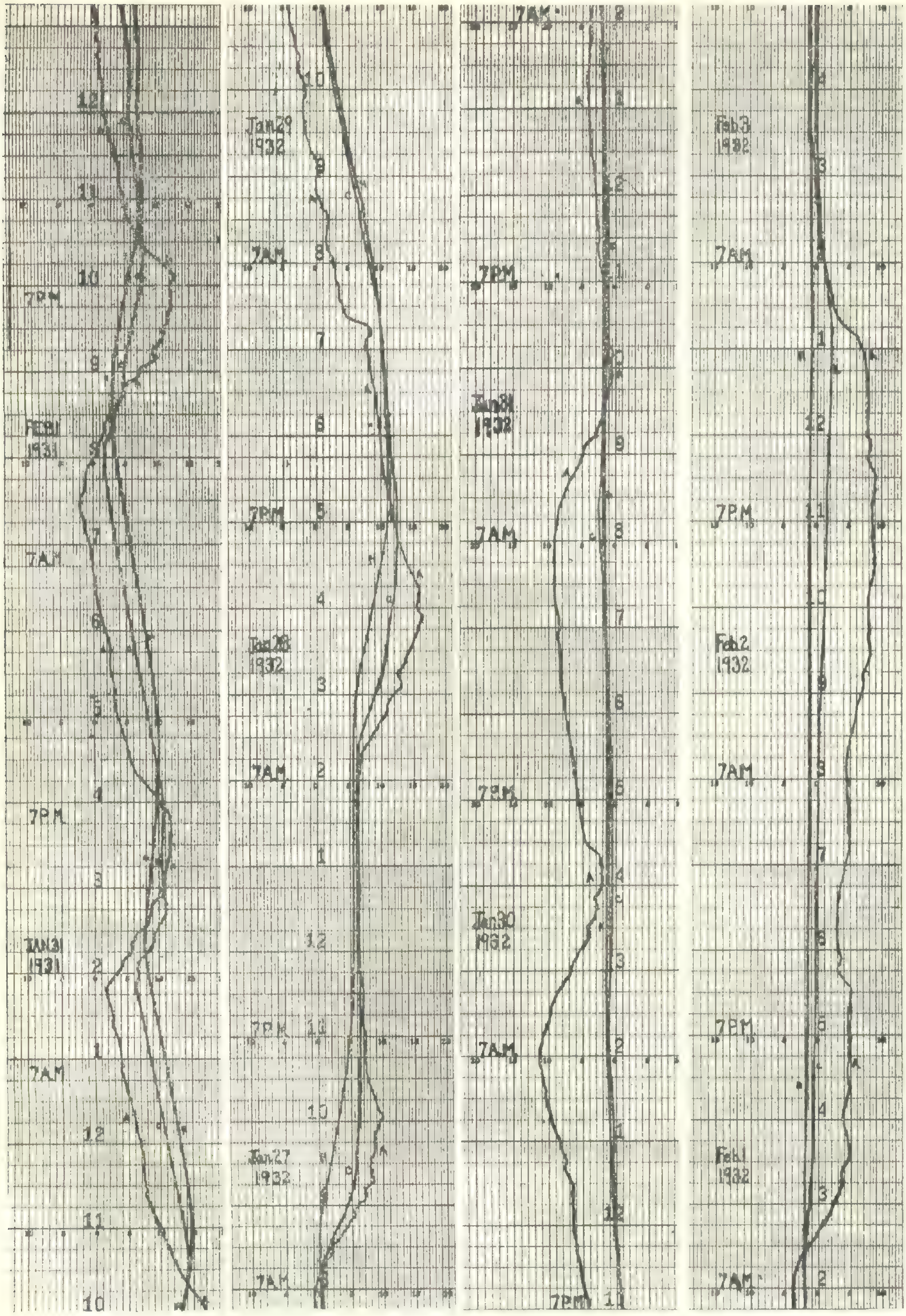
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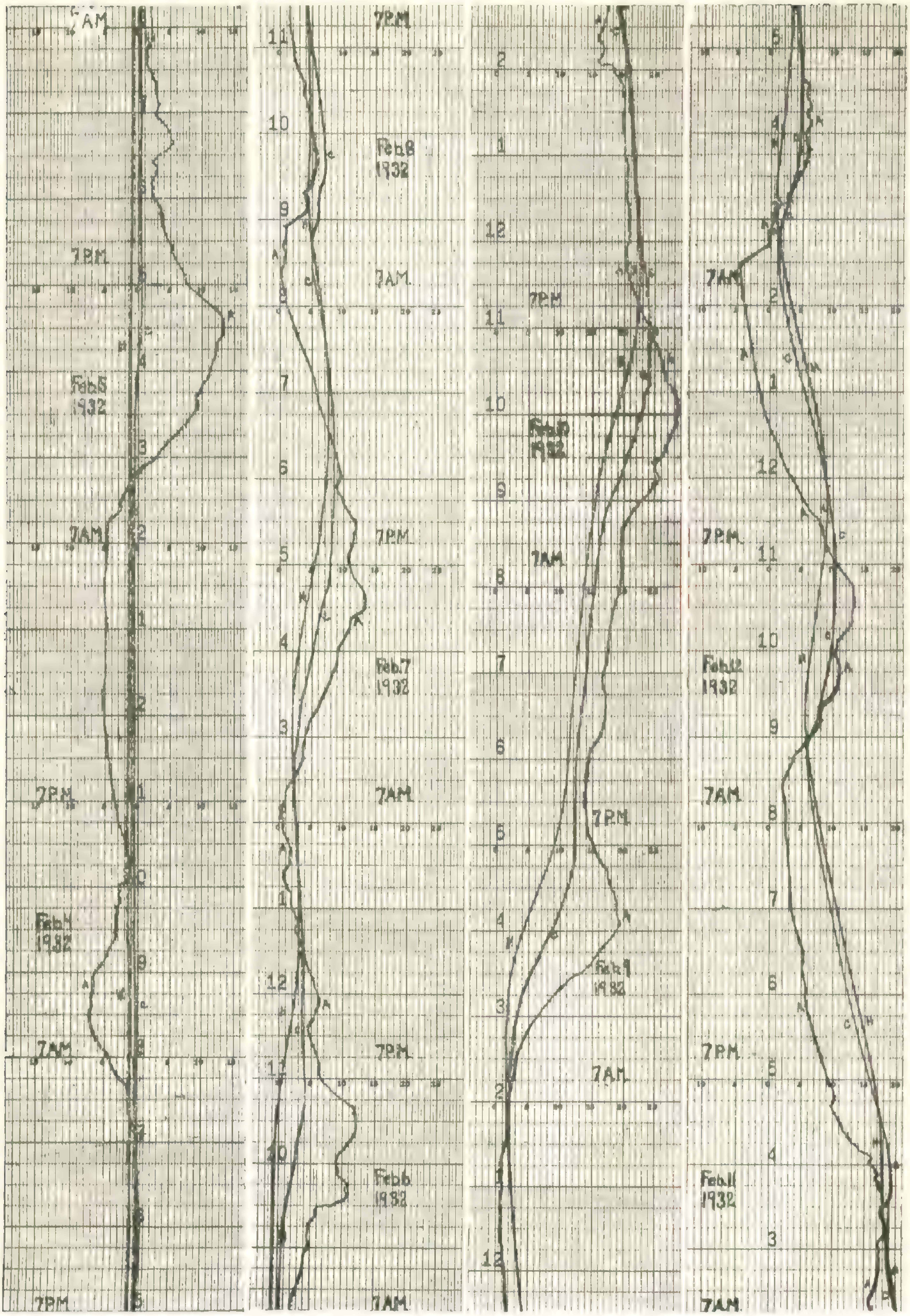
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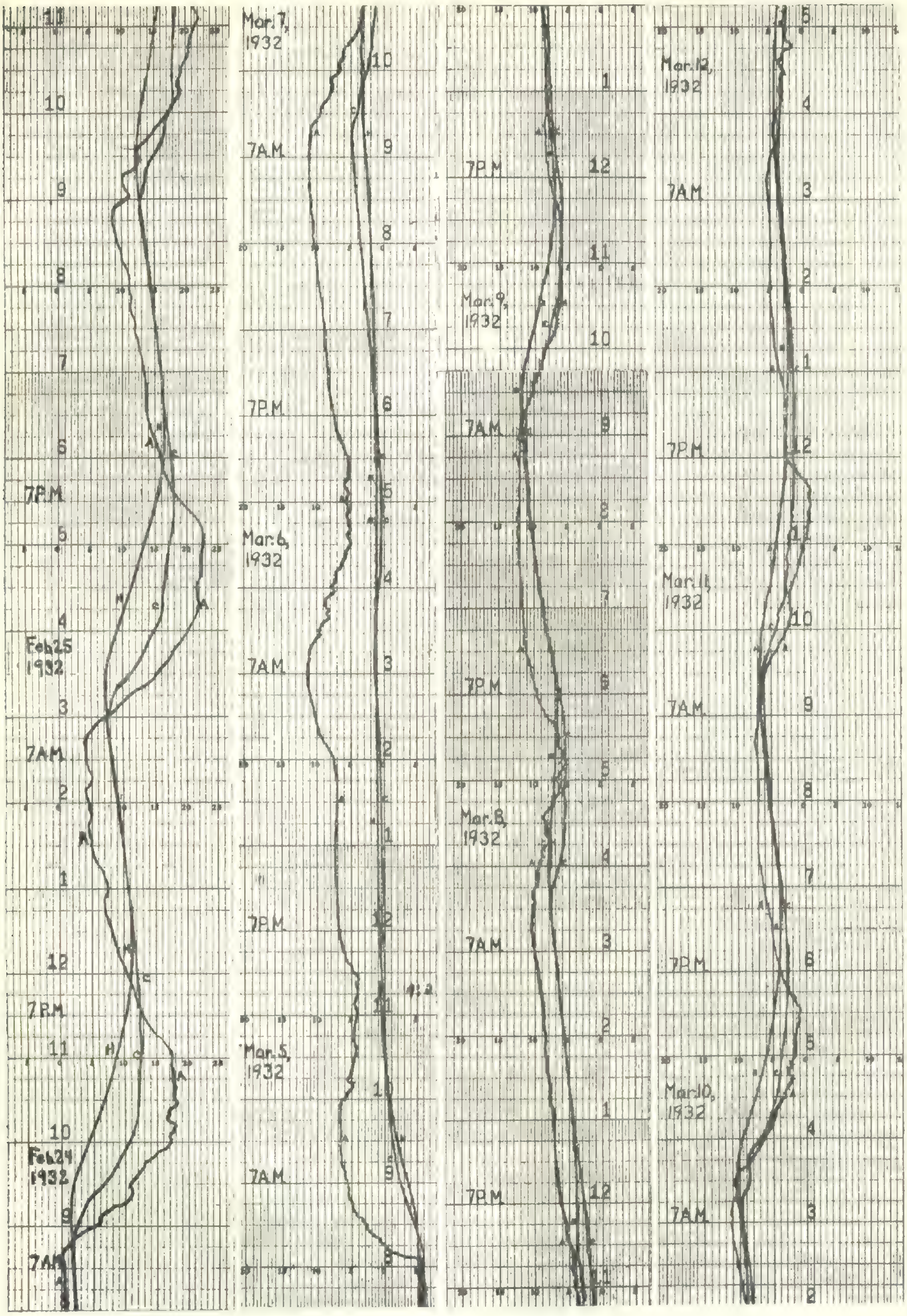
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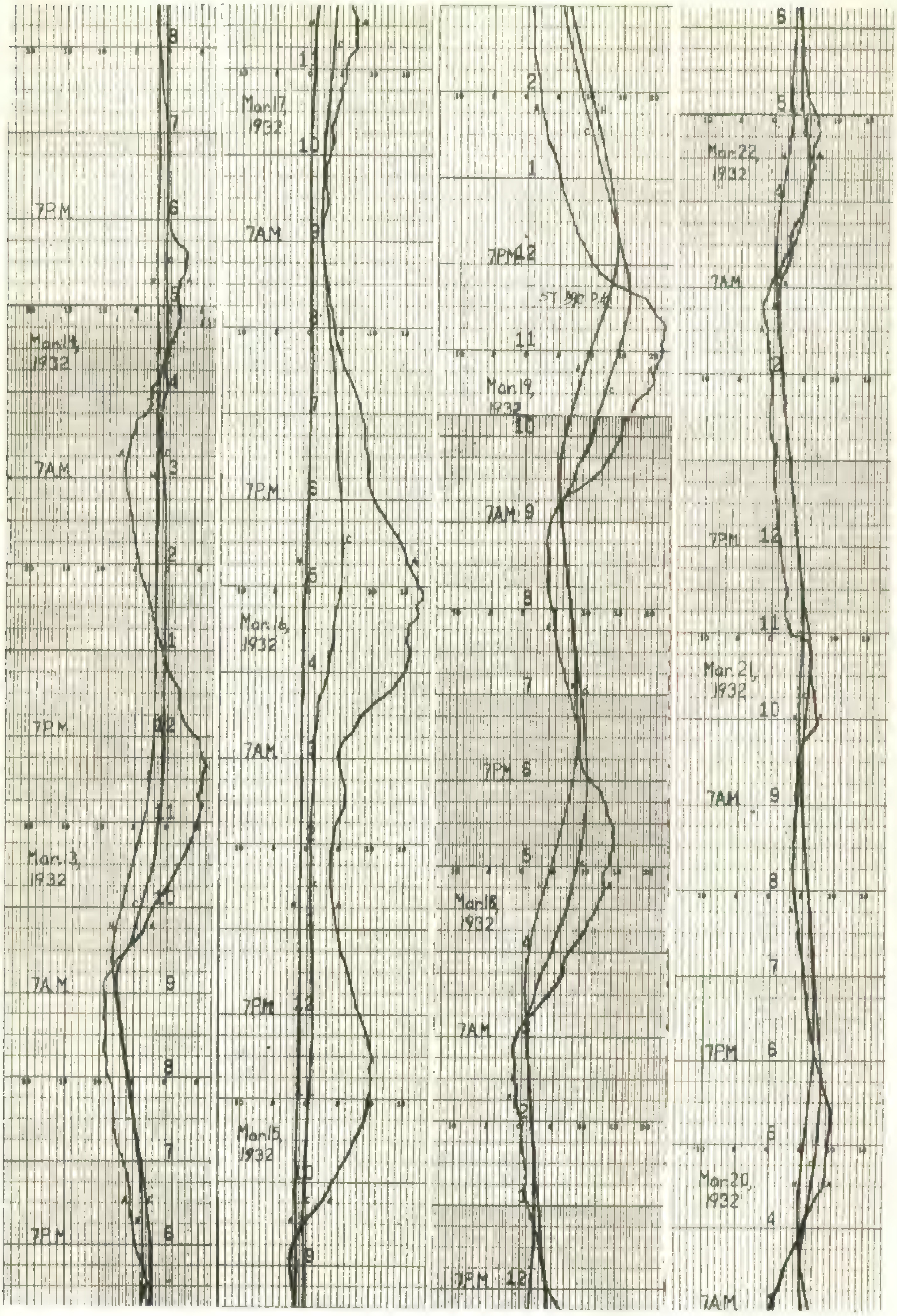
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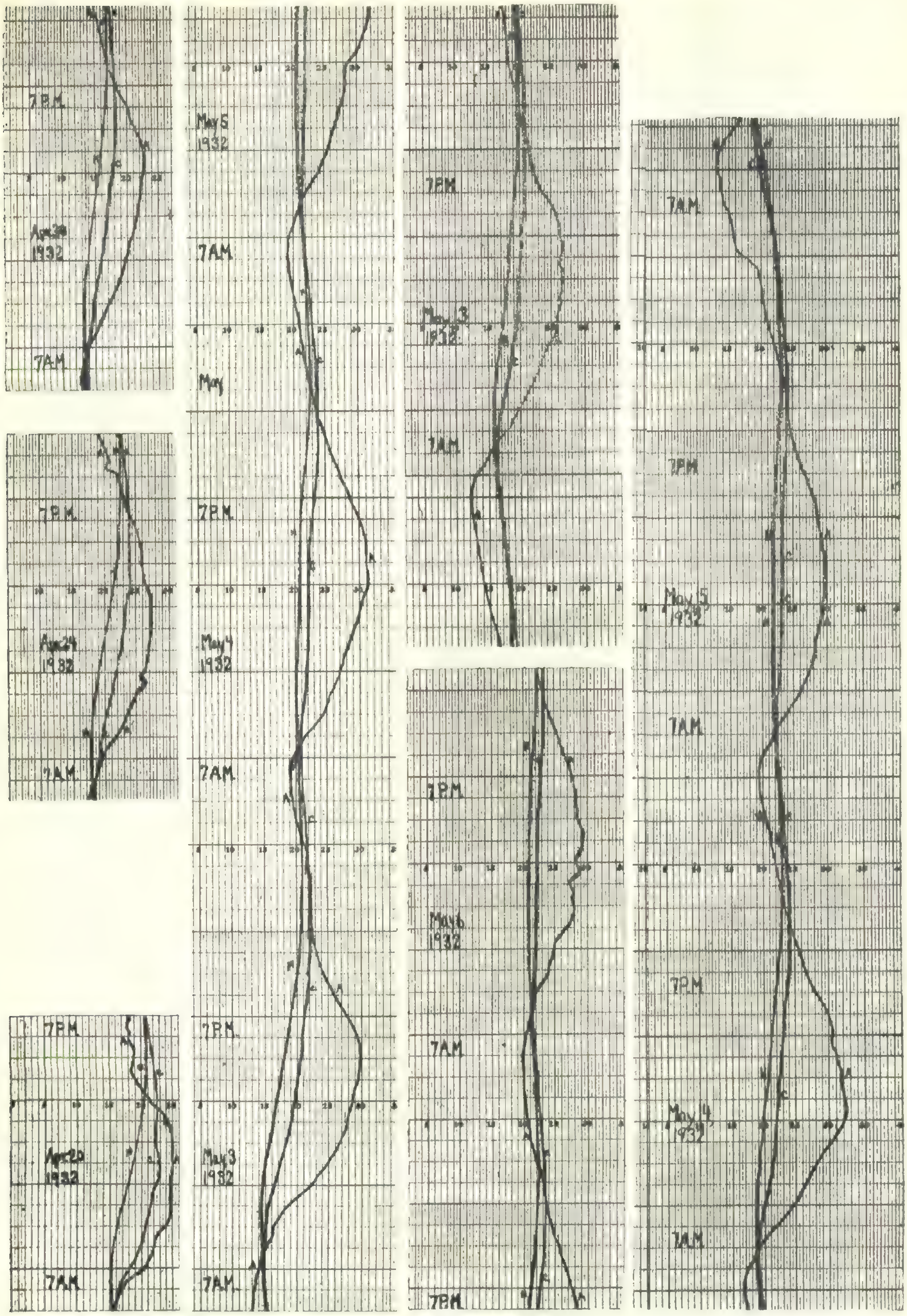
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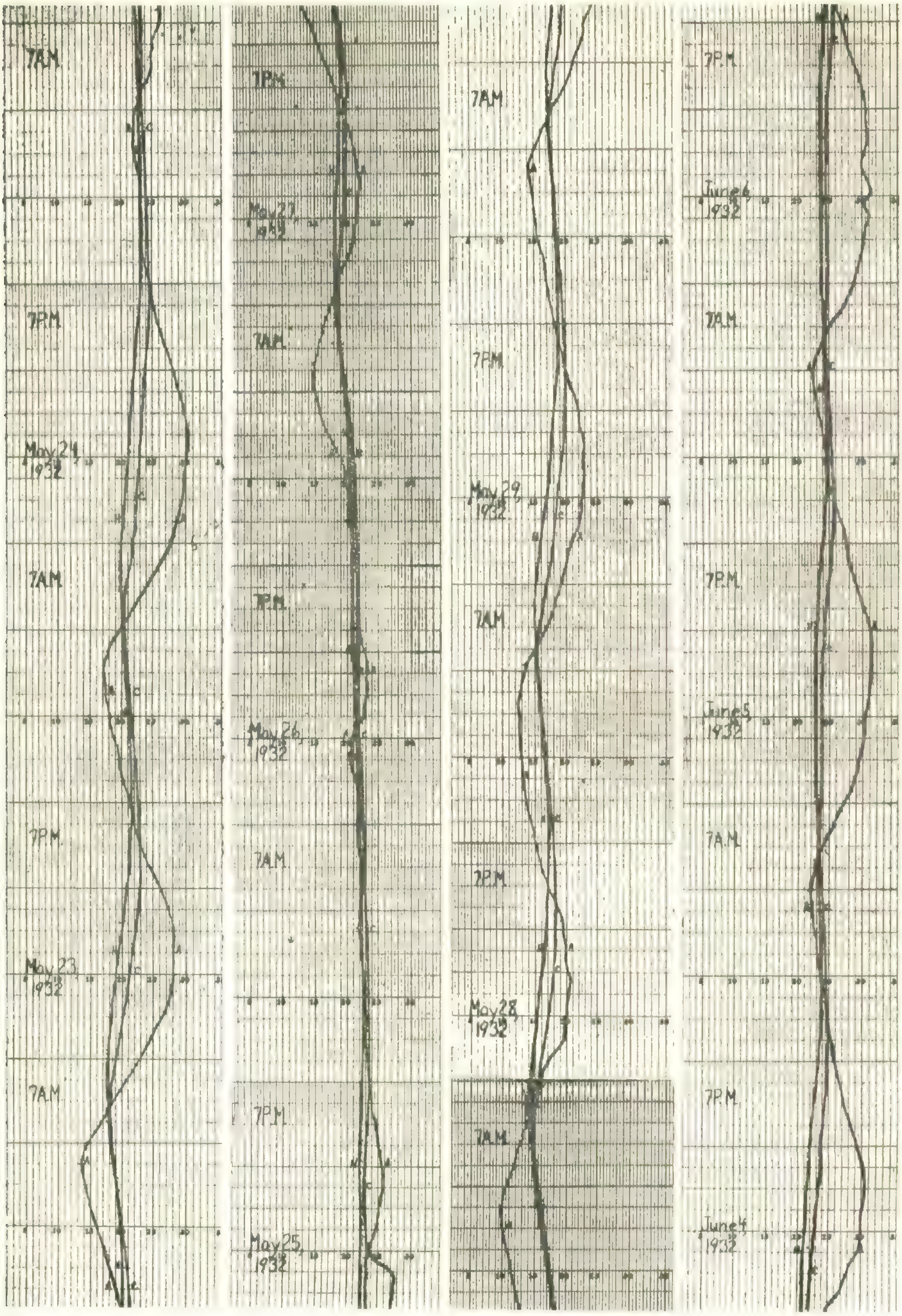
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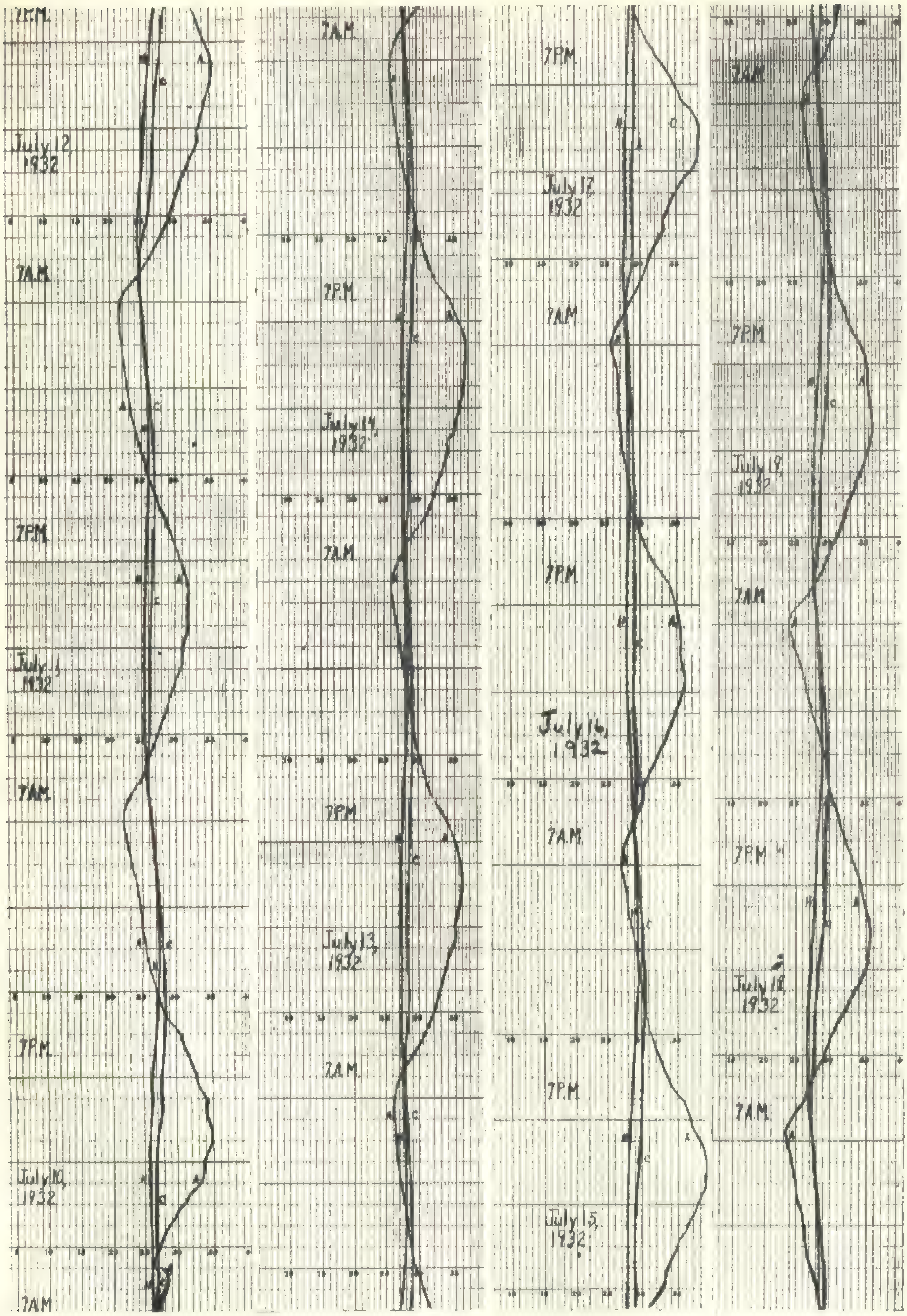
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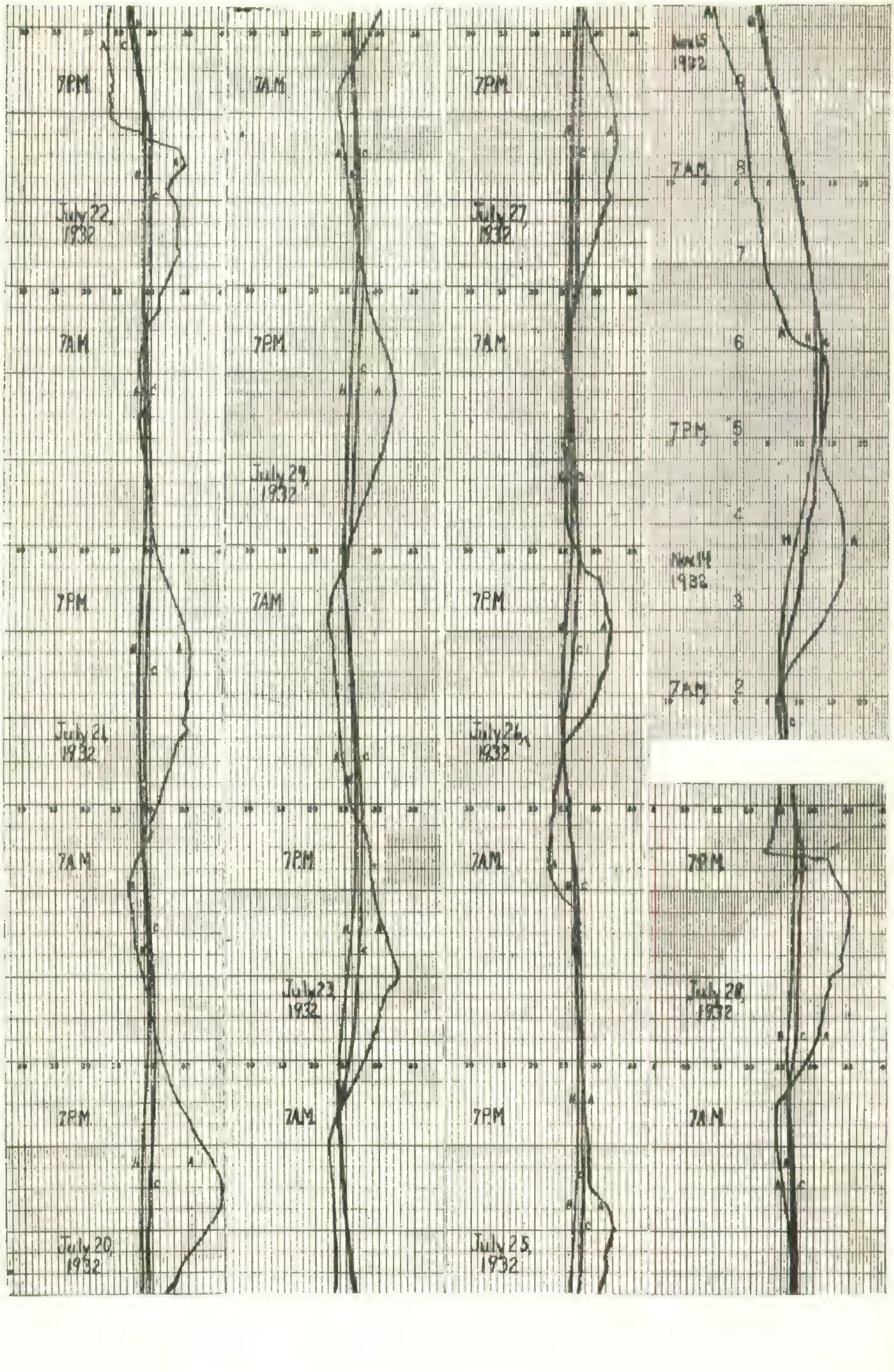
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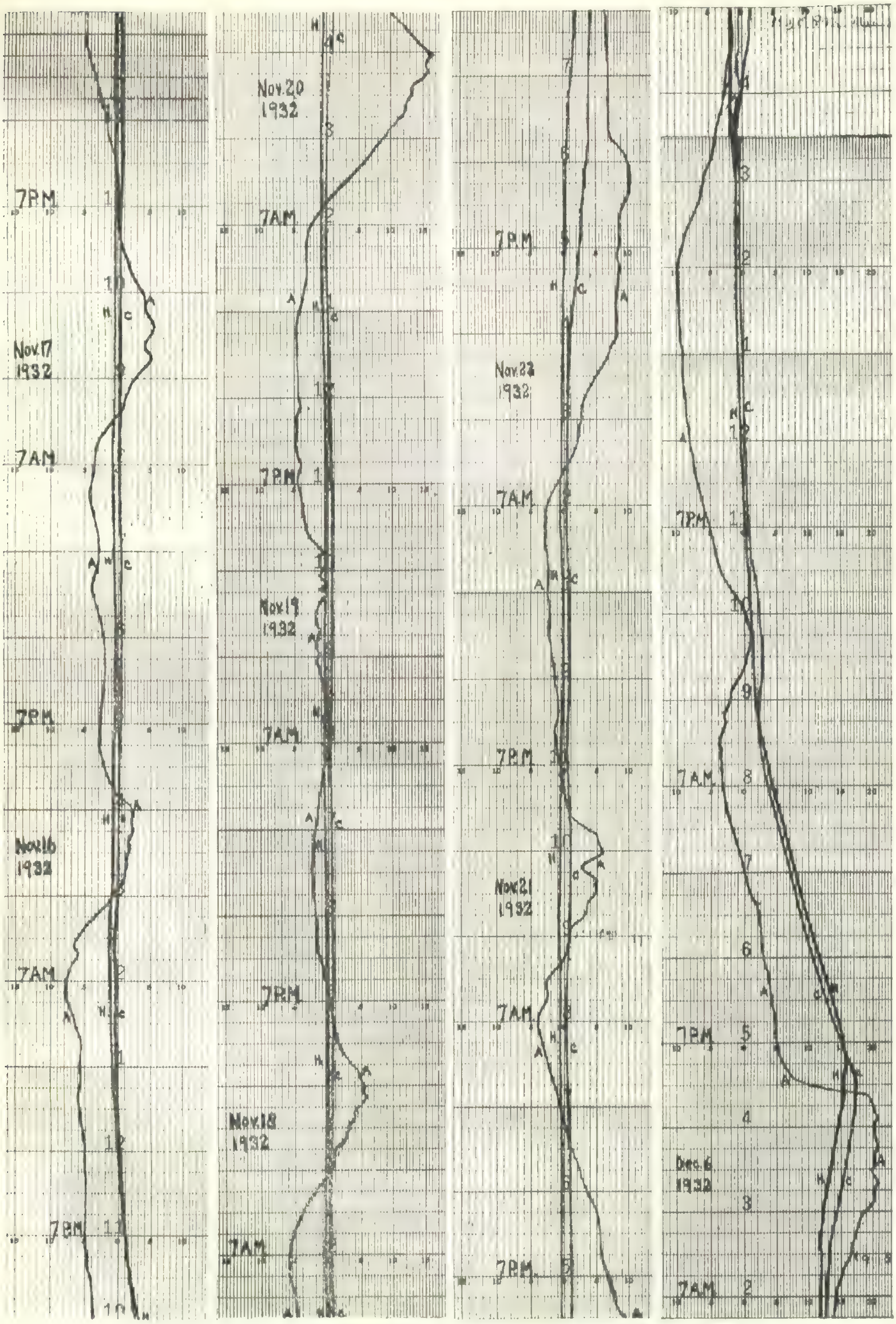
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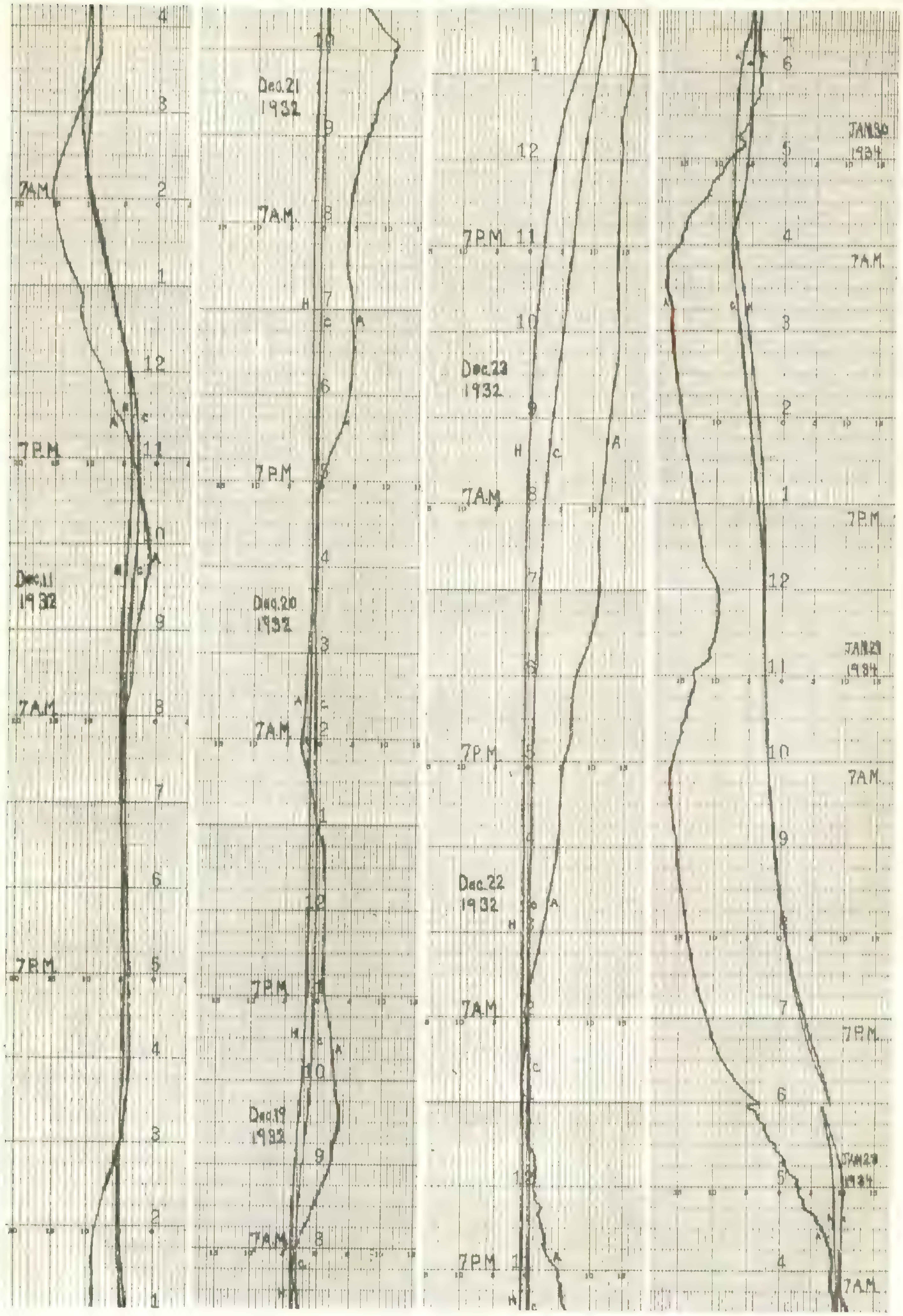
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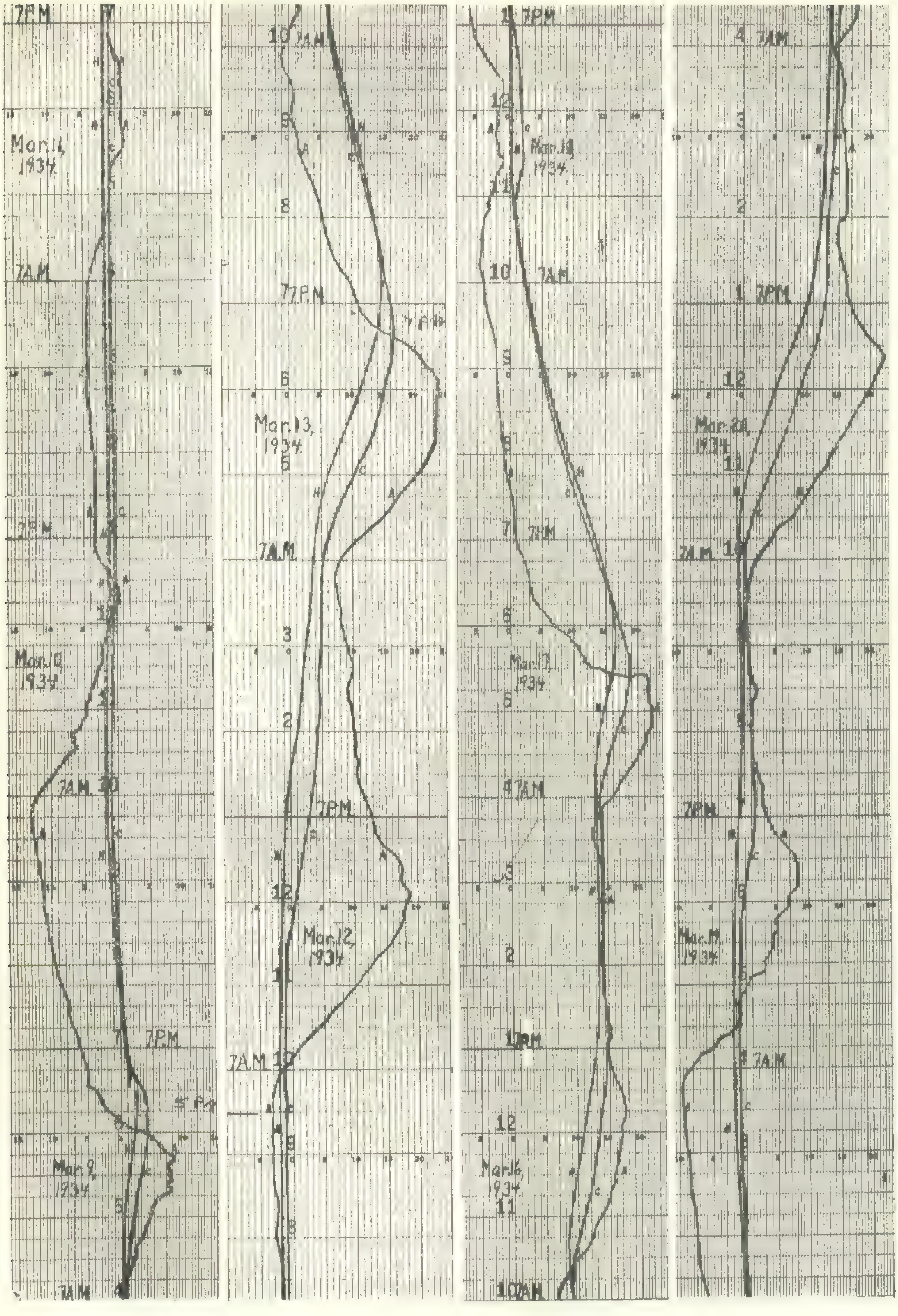

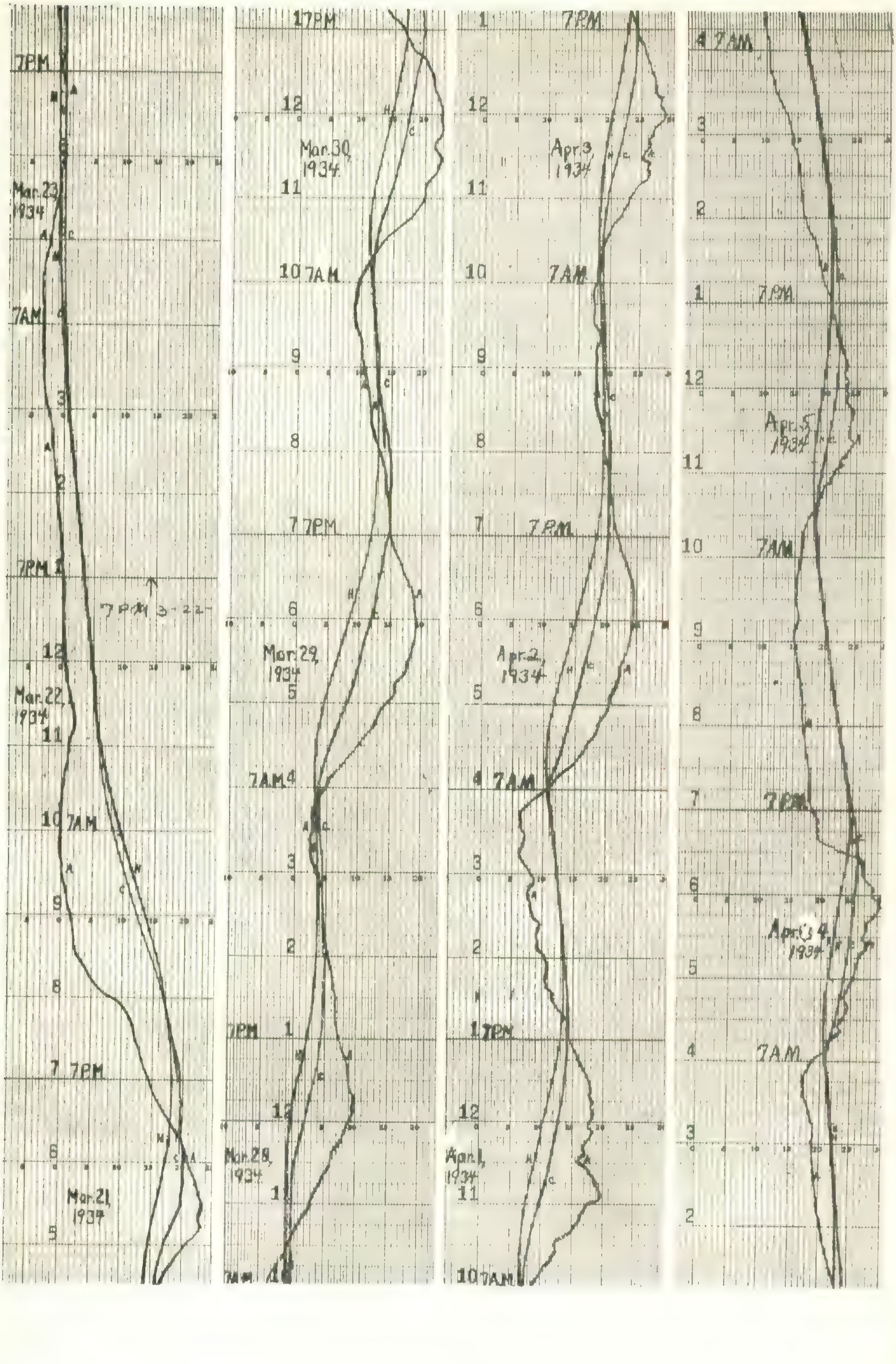
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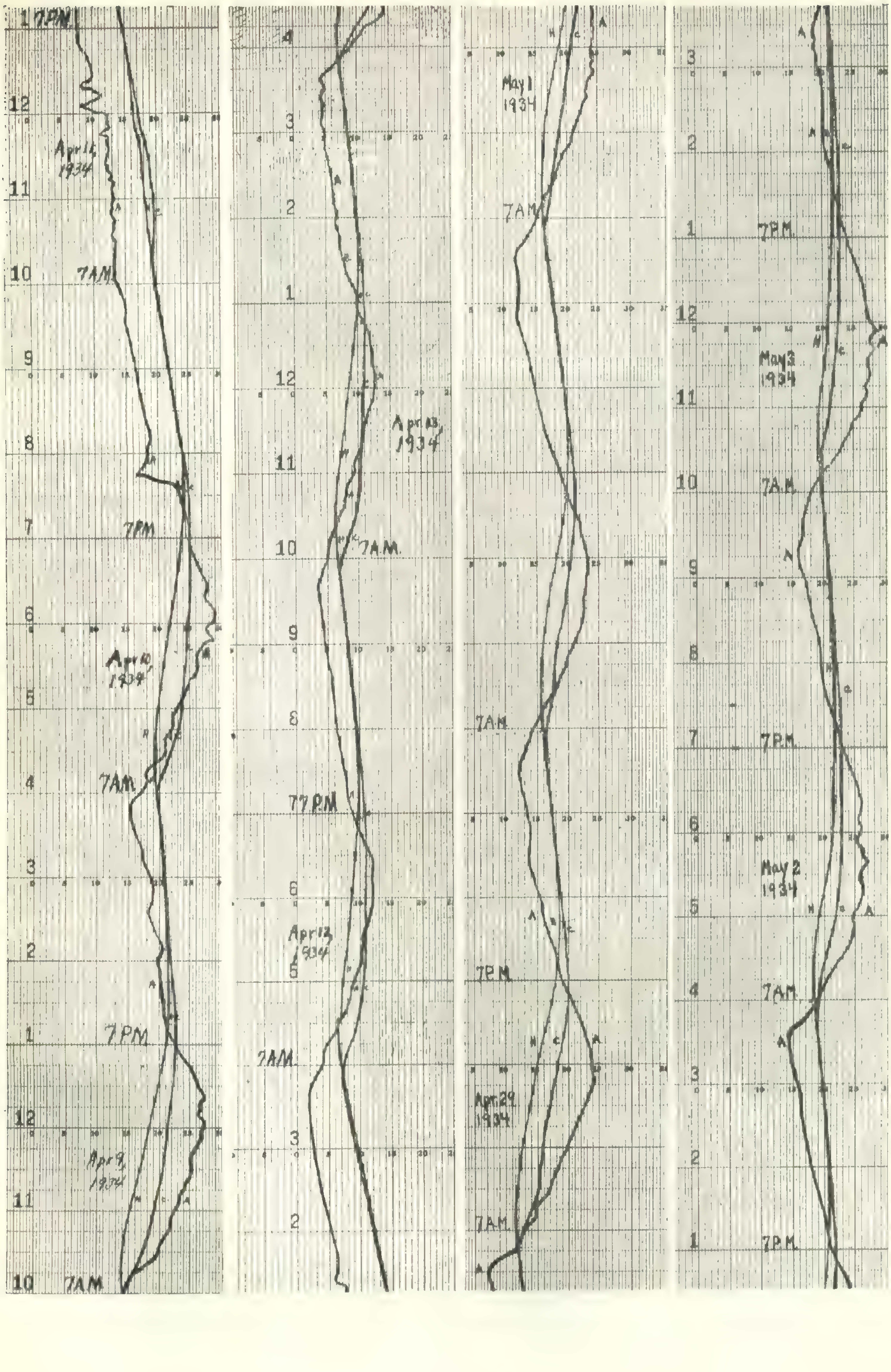
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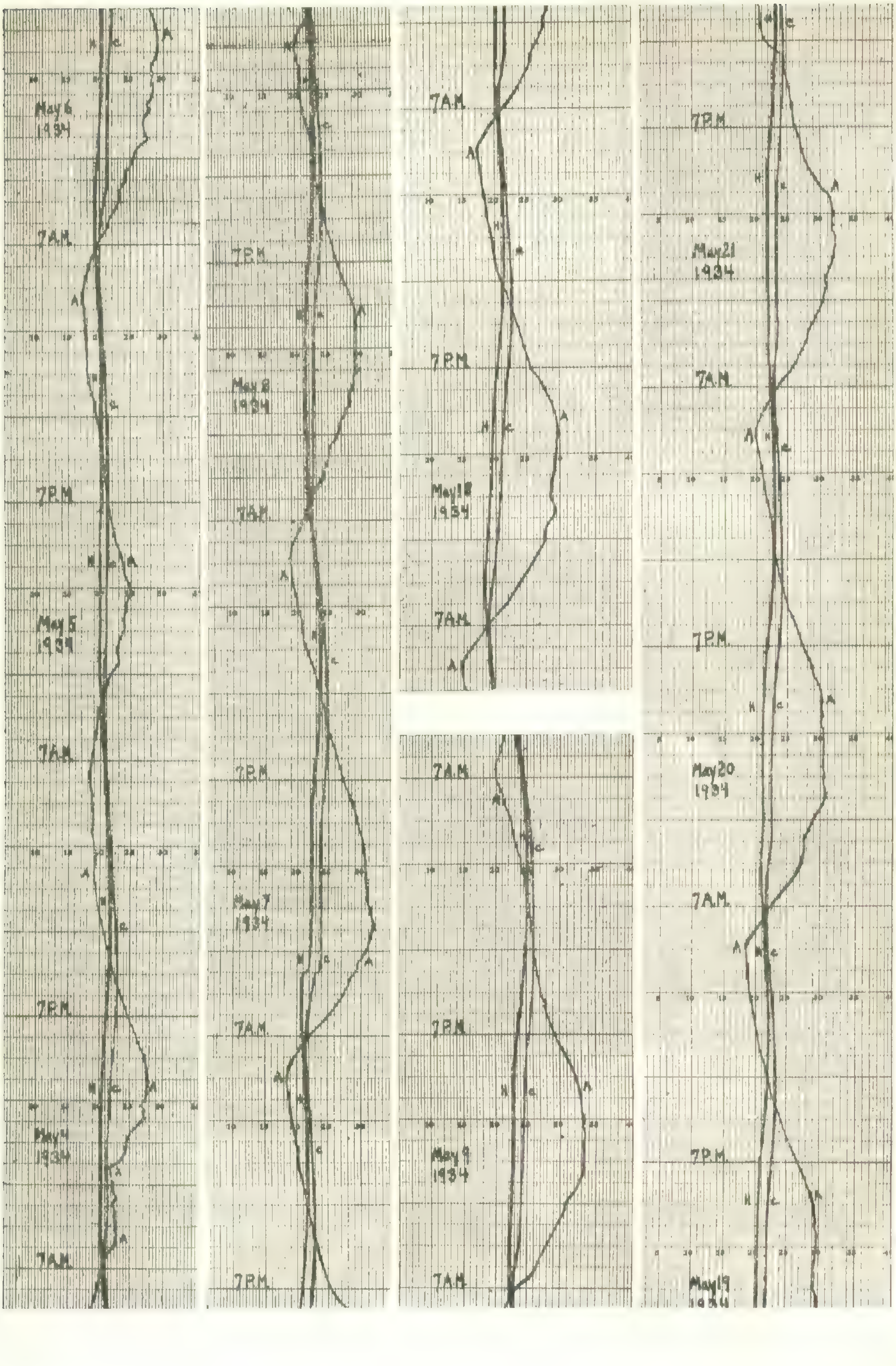
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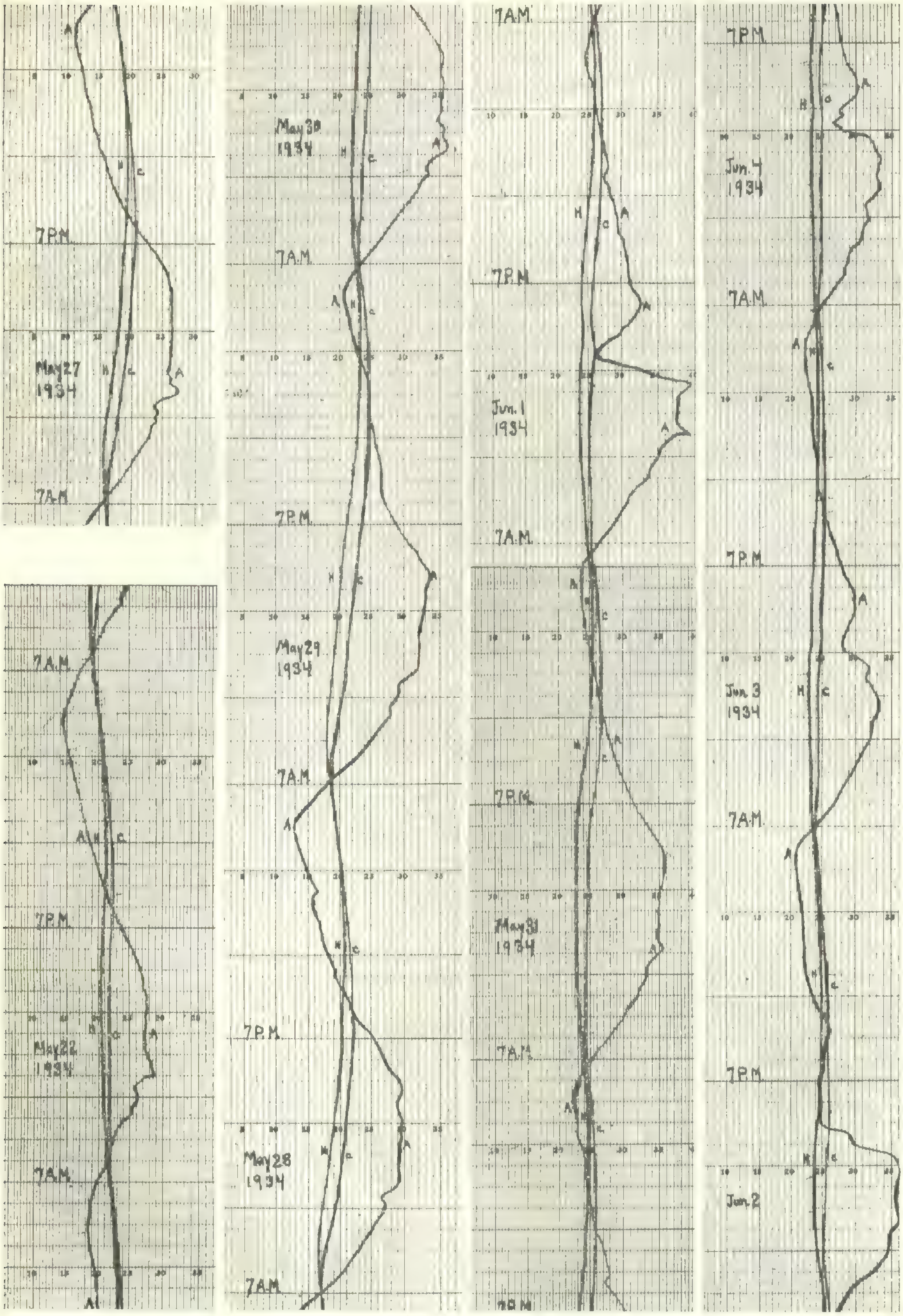
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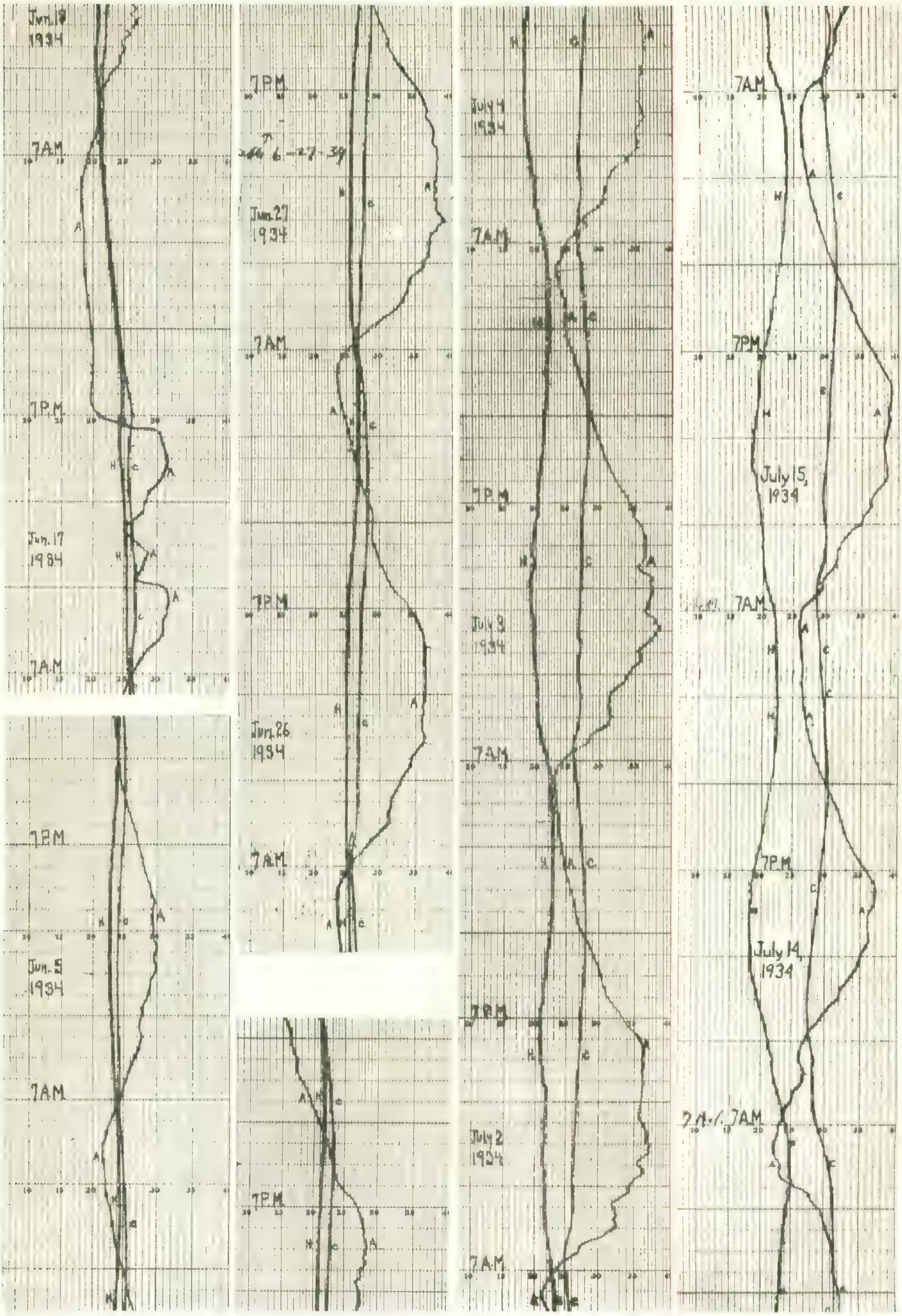
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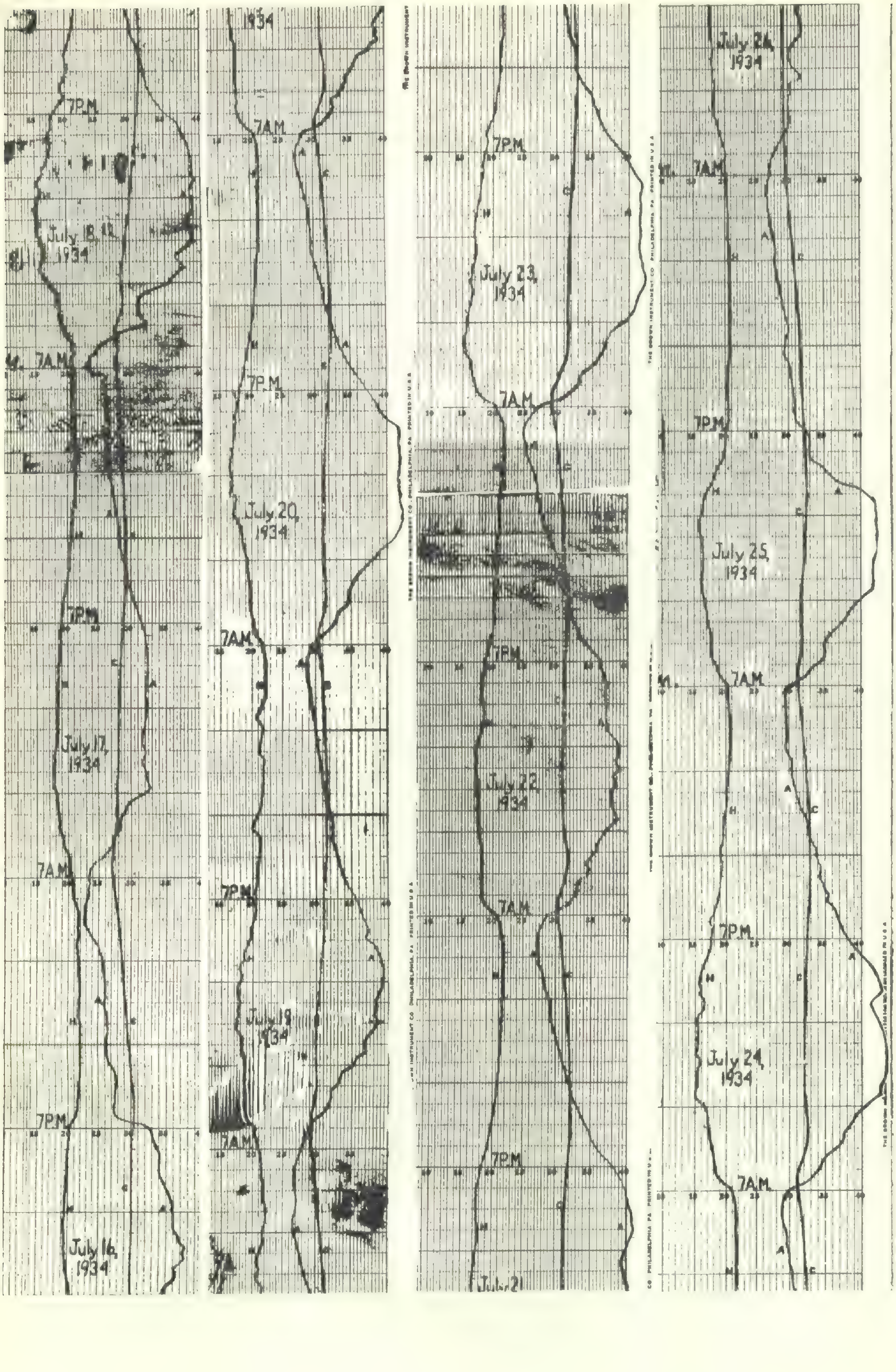
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NEW OR OTHERWISE NOTEWORTHY APOCYNACEAE OF TROPICAL AMERICA. VII[1]

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Assistant Professor in the Henry Shaw School of Botany of Washington University

Mortoniella Woodson, gen. nov. Apocynacearum (Plumerioideae-Alstoniinae). Calyx 5-partitus eglandulosus; laciniae scariaceae vel paullulo foliaceae imbricatae sat aequales mox caeduces. Corolla salverformis; tubus gracilis basi paulo gibbosus ibique staminigerus; limbi laciniae 5 paulo inaequales aestivatione sinistrorsum convolutae. Stamina 5 epipetala profunde inclusa; antherae inter se liberae 4-loculares omnino fertiles nullomodo appendiculatae; filamenta perbrevia. Ovarii carpella gemina basi distincta apice in stylo aequilongo turbinato producta, ovulis 12, 4-seriatim superpositis; stigma breviter fusiformi-capitatum. Nectaria nulla.—Arbores vel frutices (?). Folia alternata petiolo medio glandulo-umbonato caeterumque eglandulosa integra penninervia. Inflorescentia terminalis thyrsiformis.

Mortoniella Pittieri Woodson, spec. nov.; arborea vel fruticosa (?); foliis alternatis longe petiolatis oblongo-ellipticis apice longiuscule subcaudato-acuminatis basi acute obtuseque cuneatis 10–13 cm. longis 2.0–3.2 cm. latis membranaceis omnino glabris dense subhorizontaliterque nervosis, petiolo ca. 2.5 cm. longo medio glandulo-umbonato; inflorescentiis thyr-

[1] Issued November 30, 1939.

soideis terminalibus plurifloris 2.5–6.0 cm. longis; pedicellis 0.5–0.7 cm. longis; calycis lobis late ovatis vel ovato-oblongis obtusis 0.15 cm. longis extus minute puberulis; corollae salverformis tubo 1.5–2.0 cm. longo basi ca. 0.12 cm. diam. deinde paululo gibboso-inflato fauces versus gradatim ampliato extus glabro intus basi villoso-barbato caeterumque glabro, lobis oblique obovato-oblongis rotundatis paulo inaequilateralibus 1.7–2.0 cm. longis 0.5–0.7 cm. latis patulis; antheris compresse ellipsoideis 0.15 cm. longis; ovariis compresse ovoideis ca. 0.1 cm. longis glabris; stigmate 0.1 cm. longo; fructu ignoto.—Costa Rica: bois de la baie de Salinas, July, 1890, *H. Pittier 2912* (Herb. Inst. Bot. Lausanne, type).

It is most unfortunate that both the habit and the fruit of this remarkable plant are unknown. I suspect that it is rather closely related to *Aspidosperma,* but it is without a gynoecial nectary, and both the caducous calyx-lobes and the peculiar petiolar glands are quite unlike anything in the Apocynaceae known to me. The aspect of the specimen somewhat resembles *Vallesia,* but the number and arrangement of the ovules are quite different, of course, and the characteristic intrapetiolar glands of the latter genus are lacking. The genus is named in honor of Mr. C. V. Morton, of the United States National Herbarium, who called to my attention the type specimen, which had long remained unidentified in the Institut de Botanique of the University of Lausanne.

Prestonia **dentigera** Woodson, sp. nov. Frutex volubilis omnino glabrus altitudine ignotus, ramulis gracillimis internodiis ca. 15–18 cm. longis; foliis obovatis vel obovato-oblongis apice rotundatis et abruptissime breviterque apiculatis basi late obtusis 15–17 cm. longis 7.5–9.0 cm. latis membranaceis, petiolo 1.0–1.5 cm. longo; inflorescentiis lateralibus, pedunculo sterili 5 cm. longo, ramis florigeris 3 cm. longis, bracteis setaceis vix 0.1 cm. longis, pedicellis geminis 1 cm. longis; calycis lobis oblongo-lanceolatis acuminatis foliaceis plus minusve purpurissatis 0.5–0.6 cm. longis, squamellis late dentiformibus apice minutissime erosis; corollae ut dicitur flavidulae saturateque rubrae tubo 1.5 cm. longo basi ca. 0.25 cm. diam., lobis

late dolabriformibus minute apiculatis 0.8 cm. longis patentibus; appendicibus epistaminalibus oblongis vix inclusis; antheris oblongo-sagittatis 0.6 cm. longis dorso minutissime puberulis apice paulo exsertis; ovariis ovoideis ca. 0.15 cm. longis glabris; stigmate subcapitato-fusiforme 0.15 cm. longo; nectariis carnosis conspicue dentiformibus compresse ovoideis basi vix concrescentibus apice distincte acuteque lobatis basi vix concrescentibus; folliculis ignotis.—COSTA RICA: vicinity of El General, Prov. San José, alt. 640 m., Jan., 1939, *A. F. Skutch 3864* (U. S. National Herb., TYPE).

This species is closely related to *P. concolor* (Blake) Woods. and *P. obovata* Standl., but differs from both in the trichotomous inflorescence and the very peculiar, tooth-shaped nectaries.

MESECHITES TRIFIDA (Jacq.) Muell.-Arg. var. **tomentulosa** Woodson, var. nov., a varietate typica planta tota corolla excepta dense minuteque tomentulosa differt.—BRAZIL: Taperinha bei Santarem, im Bestand der *Montrichardia arborescens* kletternd, July 10, 1927, *A. Ginzberger 351* (Herb. Field Mus., TYPE). Recalling *M. bicorniculata* (Rusby) Woods., but with the floral dimensions of typical *M. trifida.*

TWO NEW ASCLEPIADS FROM THE WESTERN UNITED STATES[1]

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During the preparation of a revision of the North American species of *Asclepias*, two novelties from the western United States have been encountered which it seems well to record, since the date of publication of the complete work is uncertain.

Asclepias **Davisii** Woodson, spec. nov. (fig. 1). Herbae perennes parvulae subsucculentae prostratae; caules basi fasciculati 1.0–1.5 dm. longi plus minusve compressi simplices glabri; folia opposita late ovata vel ovato-elliptica apice obtusa vel abrupte breviterque acuminata basi late obtusa aut rotundata aut late obscureque cordata non rarius plus minusve decurrentia cum petiolo ca. 0.2–0.4 cm. longo 3.0–4.5 cm. longa 1.5–4.0 cm. lata inferne multo minora dilute viridia plus minusve glaucescentia glabra; inflorescentia terminalis umbelliformis 5–15-flora sessilis, foliis minoribus 1–2 subtendentibus, pedicellis 2 cm. longis glabris; calycis lobi elliptico-lanceolati acuminati 0.6 cm. longi sparse pilosuli; corollae rotatae dilute luteo-viridis lobi patuli ovato-elliptici late acuti 1.0–1.2 cm. longi 0.6–0.7 cm. lati intus papillati vel minute pilosuli extus apicem versus plus minusve purpurissati; staminum columna carnosa ca. 0.3 cm. alta, antherae 0.25 cm. longae dilute viridulae apicibus scariaceis obtusis inflexis, alis aequilateralibus late obtusis integris, coronae foliolae calceolatae carnosae livide purpurissatae 0.5 cm. longae 0.35 cm. latae compressae prope margines interiores ca. 0.1 cm. longae abrupte apiculatae basi columnam totam adnatae, corniculo incurvato adnato omnino incluso vel nullo; pollinia ca. 1.5 mm. longa compressa anguste inaequilateraliterque pyriformia, caudiculis gracilibus tortulis ca. 0.5 mm. longis, corpusculo compresse rhomboideo ca. 0.25 mm. longo; folliculi non visi.

[1] Issued November 30, 1939.

Idaho: Glenn's Ferry, Elmore County, May 15, 1938, *R. J. Davis 85* (Herb. Missouri Bot. Garden, type); Oregon: loose soil, high hillsides opposite Lloyd Humphrey's ranch, Grant County, April 30, 1925, *L. F. Henderson s.n.* (Herb. Missouri Bot. Garden).

Professor Davis writes me: "The plant grows prostrate on the ground with nothing but the ends of the branches turned slightly upward. The stem is a pale green color, but I did not

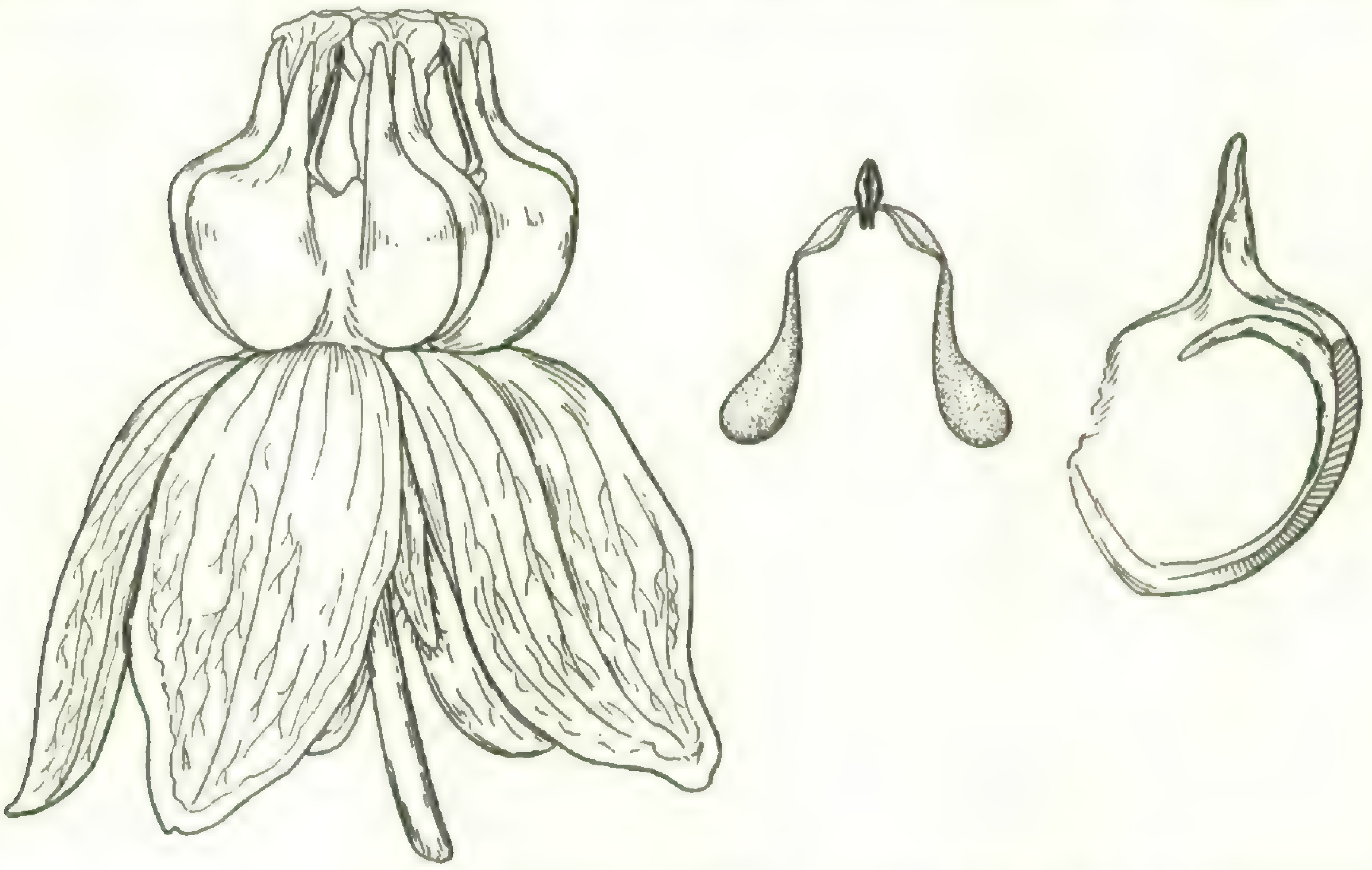

Fig. 1. *Asclepias Davisii* Woodson. Flower, pollinia, and hood in longitudinal section. (Drawn by A. A. Heinze.)

look particularly to see whether it was flattened or not. . . . It seems to grow only on barren alkaline clay knolls. There was no plant of it found growing where any other vegetation grew."

A. Davisii closely simulates *A. Cryptoceros* Wats. in general appearance and distribution and is doubtless closely related to it. In the former, however, the corona hoods are more abruptly apiculate and scarcely attain the anther-head which they considerably surpass in the latter, where the flowers are somewhat larger as well.

The two specimens cited, although essentially similar, show certain dissimilarities of the corona: the hoods of *Davis 85* are more abruptly and shortly apiculate and are without the

inconspicuous, incurved horn characteristic of *Henderson s.n.* The character of the horn appears to be unusually inconstant in certain species of the western United States, notably in *A. californica* where I have observed a series of intergradations from a very definite structure to complete obsolescence. Similar variation is shown strikingly in the following species as well.

Asclepias **Cutleri** Woodson, spec. nov. (fig. 2). Herbae perennes parvulae; caules basi fasciculati suberecti 1–2 dm.

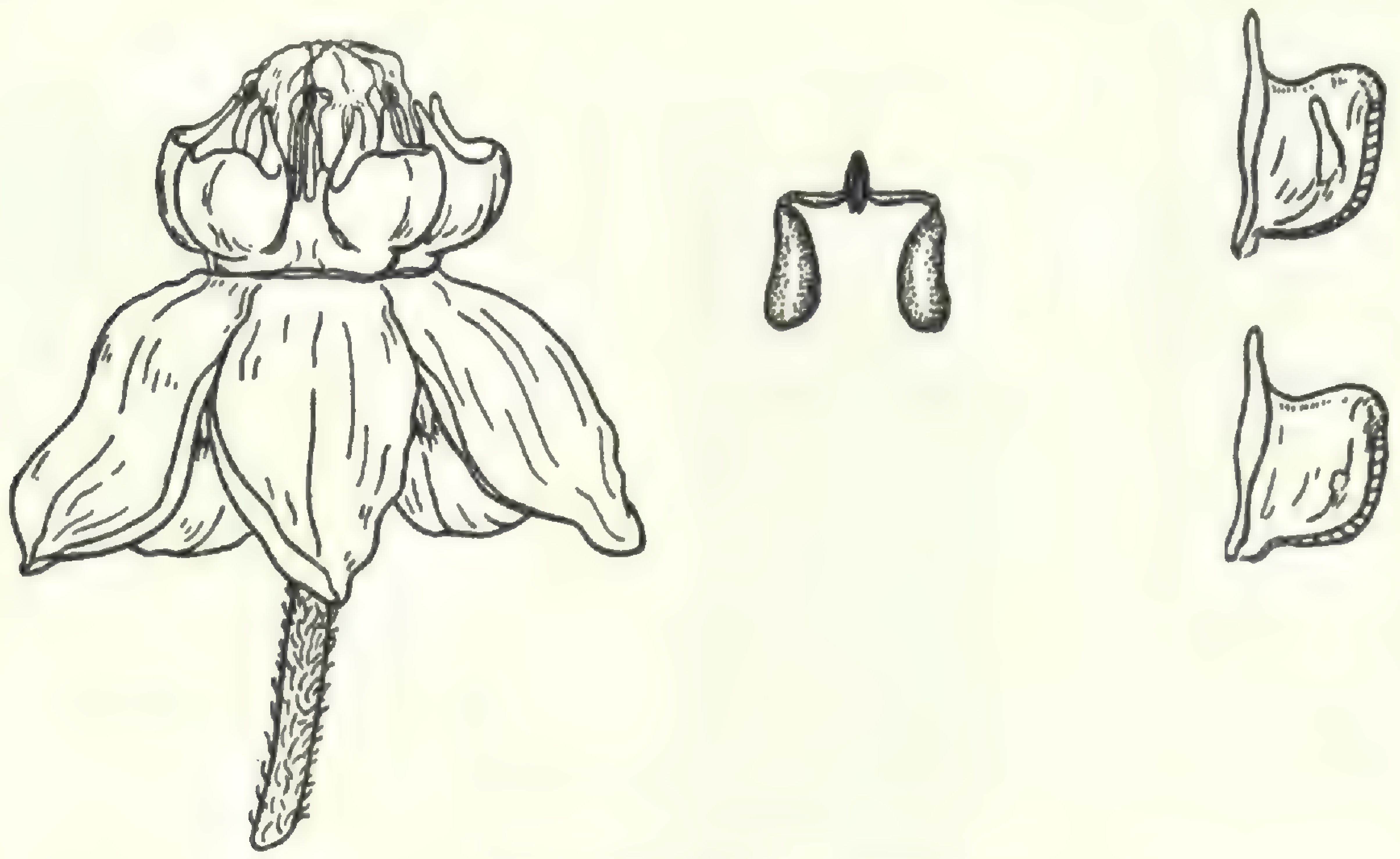

Fig. 2. *Asclepias Cutleri* Woodson. Flower, pollinia, and two hoods in longitudinal section to show variation of the horn. (Drawn by A. A. Heinze.)

alti tenues simplices vel rarius pauciramosi minute pilosuli; folia opposita vel approximata subsessilia linearia apice acuminata basi attenuata cum petiolo vix bene manifesto 4–8 cm. longa ut videntur subsucculenta minute pilosula dilute viridia; inflorescentia in axillis foliorum lateralis pauciflora brevissime pedunculata vel verisimiliter sessilis, pedicellis ca. 1 cm. longis minute pilosulis; calycis lobi ovato-lanceolati acuminati dense pilosuli; corollae rotatae dilute lividae lobi patuli ovato-elliptici late acuti 0.5–0.6 cm. longi ca. 0.2 cm. lati extus minute sparseque pilosuli intus minutissime papillati; staminum columna carnosa ca. 0.1 cm. alta inter foliolas coronae saccata, antherae 0.15 cm. longae apicibus scariaceis obtusis inflexis,

alis obtusis integris; pollinia compresse subrhomboideo-pyriformia ca. 0.75 mm. longa, caudiculis corpusculoque ca. 0.25 mm. longis, coronae foliolae saccatae carnosae 0.15 cm. longae dorso obtusae, lobulis lateralibus acutis prominentibus, corniculo parvo vel subnullo incluso; folliculi penduli ovato-fusiformes ca. 5 cm. longi dense pilosuli.

Arizona: rare on sands, 5 mi. west of Rock Point, Apache County, June 15, 1938, *H. C. Cutler 2177* (Herb. Missouri Bot. Garden, type).

This species obviously is most closely related to *A. brachystephana* Engelm. and *A. uncialis* Greene, from both of which it differs in its habit and narrower foliage, as well as in technical details of the gynostegium. Perhaps most noteworthy is the fruit, since pendulous follicles previously have been known to occur only in *A. perennis* and *A. albicans* amongst the species of the United States.

CONTRIBUTIONS TOWARD A FLORA OF PANAMA[1]

III. Collections during the Summer of 1938, chiefly by R. E. Woodson, Jr., P. H. Allen, and R. J. Seibert

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AND RUSSELL J. SEIBERT

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During the summer of 1938, from June 17 to August 20, a party consisting of R. E. Woodson, Jr., Paul H. Allen, and Russell J. Seibert was sent to Panama under the joint auspices of the Missouri Botanical Garden and the Arnold Arboretum of Harvard University. The purpose of the expedition was chiefly to recoup the losses sustained in a fire at the end of the previous summer's collecting trip.

As in previous years, numerous short trips into the interior were made from the Tropical Station of the Missouri Botanical Garden at Balboa, C.Z., now under direct control of the Canal Zone. The principal trips, however, were to the highlands on Chiriquí on the Pacific slope of the Volcán de Chiriquí, a favorite collecting locality since the days of Seemann and Warscewicz, and the lowlands about the Chiriquí Lagoon in Bocas del Toro, upon the Atlantic slope. A projected trip to Darién was necessarily postponed because of the illness of both Woodson and Seibert. This trip was taken later in the year by Allen, and will be reported in the next of this series.

Although it is still possible to make the trip to Chiriquí rather painfully by cattle boat, use of the airplane and the new Panamerican Highway has decided advantages. Regular flying service from Panama City to David, the capitol city of Chiriquí province, reduces the time between the two cities, from a day and a night via the lowing and odorous hulls of the Compañía de Navegaciónes Chitreana, to a mere two hours.

[1] Issued November 30, 1929.

Air travel, however convenient, has its drawbacks for the botanist. Many miles of vegetation-covered wilderness is given an exasperatingly distant enchantment. And should he be a timid soul, the wilderness becomes forbidding indeed if a precipitant descent is contemplated. In 1935 Woodson and Seibert, together with Dr. George W. Martin, had a taste of such interest when the landing gear of their plane was wrecked at the very moment of take-off, on an improvised landing field at Llanos del Volcán, in Chiriquí. Safe landing at that time was made by the skill of Robert Marstrand, the pilot, who was killed on the same route later in the summer, flying headlong into the clouded summit of Cerro Trinidad.

Taking all such things into consideration, a light truck was purchased by Allen and converted into a cavernous conveyance for enough collecting and pressing materials for a month. On top of all the other paraphernalia a precarious garnish was made of a number of living ornamental plants potted in tin cans and intended for our good friend Mr. T. B. Mönniche at Boquete. The whole cargo, heaped high, was covered with water-proofed canvas, and we set upon our way.

The Panamanian section of the Panamerican Highway is known locally as the *Carretera Nacional*. The preceding summer we had made the approximately 300-mile trip from Panama City to David in an ancient, specially chartered *chiva* (a light bus, but in Spanish, appropriately, a goat). We found then that most of the western half of the road was either in the process of being blasted from solid rock or cut through jungle, and the whole trip required twenty-eight hours of continuous driving. When all other details of that trip vanish, the scientific occupants of the *chiva* will probably still remember how, during each of those twenty-eight hours, they took turns holding up the windshield with their feet for the expressed benefit of the Panameño driver, bounding over the *Carretera* in a most unnatural position.

This year, however, we not only rode in a ¾-ton truck provided with springs, but found to our delight that the road had been improved quite noticeably, enabling us to reach David

after only fourteen hours. Although the road had been much worked upon during the year's interval, the surrounding country was still unspoiled, and we were able to make numerous collections en route, including several novelties. Even from the road, for example, the bright orange flowers of *Tussacia Woodsonii* Morton, abounding in the low woods near Remedios, could be distinguished from the rather greenish yellow flowers of the common *T. Friedrichsthaliana.* So with a grinding of brakes and a tornado of dust, a new species was added to the interesting family Gesneriaceae. In the swampy jungles near the Río Fonseca the attention of any motoring botanist could scarcely miss the giant, scarlet-bracted canes of *Costus Lima* K.Sch., previously unknown from Panama. Not a hundred yards from the road we ate our lunch under a tree in which were twining *Fernaldia speciosissima* and *Prestonia remediorum,* new species of Apocynaceous lianas.

Nightfall found us established at the cavernous Pension Italiana in David. Early the next morning we abandoned the truck and transferred our gear to the narrow-gage train for the trip to Boquete. The line is only about thirty miles long, but is at such a continuous grade from David, about 50 m. elevation, to Boquete, about 1000 m., that it appeared to be all the diminutive locomotive could possibly do to pull us thence in three hours.

The name Boquete is well deserved, for it means "The Bouquet." The town, of perhaps 1,000 inhabitants, is set at about the elevation of Cartago, in Costa Rica, and is favored with a climate that is almost ideal. With the Volcán de Chiriquí towering above, it lies in a deeply forested canyon of the tempestuous little Río Caldera. Nearly everyone in town has a luxuriant garden almost monotonously filled with blooming roses, lilies and delicious strawberries. Not far up the mountain slopes a native raspberry *(Rubus glaucus* Benth.) abounds, which is really superior to the best cultivated berries of the States. It is no wonder that Boquete is a favorite alike for vacationists from the Canal Zone and for nearly all botanists who visit Panama.

But the real attraction of Boquete is that it is not far from Finca Lérida, the remarkable establishment of Mr. T. B. Mönniche, nearly 300 m. higher upon the slope of the volcano. It is doubtful whether Mr. Mönniche and his charming wife themselves know how many pilgrims to Finca Lérida they welcome each year. Surely in Panama, if not in all Central America, there is not another finca where the coffee is more successfully grown and handled, where the native help is more kindly and wisely administered, and where the proprietors are more gracious to all with whom they come in contact.

Mr. Mönniche is a keen naturalist himself, and fully understood our needs in studying the local vegetation. Accordingly, as in the previous summer, he placed at our disposal a little maintenance shed, "Casita Alta," about three miles farther up the slope of the volcano, at an elevation of about 2,000 m. Casita Alta furnishes the greatest requirement of a visiting plant collector, particularly in the rainy season: it is dry. Otherwise, it is a frame structure of about ten by eight feet, without windows, floor or furniture except a shelf in the back for our supplies. A bed is made by pulling fronds of the abundant *Pteris podophylla* Sw. *(sensu lato)*, and making a mat on the dusty floor for sleeping-bags. Fire-making and cooking, as well as the drying of specimens, must be done out of doors.

We found Casita Alta exactly as we had left it at the end of the preceding summer, even to the sprig of mistletoe hung over the door like the sword of Damocles. Immediately after unpacking our belongings that Mr. Mönniche thoughtfully had had packed up the mountain side for us by mule-train we set about the construction of a "pressing room," or rather, a canvas shelter for our press-frames. During the rainy season, at least, artificial heat is necessary for drying in the tropics. After experiments over several collecting seasons, we have found that the one-unit, pressure kerosene stoves of Swedish make are by far the hottest, safest, and most economical.

It would be difficult to find a site more attractive to the botanical collector than that of Casita Alta, since it is located within easy reach not only of the deep valley of the Río Caldera

AN ALPINE MEADOW NEAR THE SUMMIT OF VOLCÁN DE CHIRIQUÍ

THE CAMP AT CASITA ALTA, SUMMER OF 1937

headwaters, but of the higher slopes of the volcano itself. We soon found that it was a good arrangement for two of the party to go fairly far afield, leaving the third to tend the kerosene stoves. Incidentally, the one left could collect in the immediate vicinity of the camp, where much of interest was to be found, including the gigantic *Piper Gigas* Trelease, a tree 10 m. tall with a bole 30 cm. in diameter. Another very distinct pepper of similar height but more slender bole is *P. affectans* Trelease, also in this immediate vicinity. A rather rare borage, *Hackelia costaricensis* (Brand) Johnston, was so common in the immediate clearing around camp that it appeared to be an introduced weed.

After about three weeks of collecting from Casita Alta, including a trip to the summit of the volcano, we packed up our sundries, and descended to Boquete, paying our respects, en route, to the Mönniches, through whose kindness we had had such a delightful and profitable visit. The region about Boquete, aside from the Canal Zone, is probably the best known botanically of Panama. Nevertheless, things were made so convenient for us at "El Hotel Nuevo" that we could not forego a few days of foray, which resulted in the discovery of several interesting species.

Back in the Canal Zone again, several trips were made toward Chepo, to the east, and Arraiján, just over the boundary to the west. A visit of several days was made to the island of Taboga, in Panama Bay. Although the island has been a favorite resort from the mainland since the days of Spanish domination, and has been visited probably by every botanist to collect on the isthmus, a number of additions were made to the flora of Panama, including the antillean *Forsteronia spicata* (Jacq.) Meyer, which grows in veritable thickets along the northern shore.

The last two weeks of collecting were spent by Woodson in the neighborhood of Almirante, Bocas del Toro province, for a foray at the kind invitation of Dr. Wilson Popenoe and the United Fruit Company. The Atlantic slope of Panama is more poorly known botanically than the Pacific, and this port had

been selected because bi-monthly sailings are made to it from Cristobal by the ships of the Fruit Company.

The trip to Almirante was made with some misgivings, since the place has a rather evil reputation in the Canal Zone as a disease-infested shambles of abandonment caused by the plague of the Panama Disease of bananas. It is quite true that the disease has almost completely wiped out the traffic in bananas at Almirante, but the growing and processing of cocoa and abacá is progressing under very efficient management, and will doubtless restore the importance of the port.

Almirante itself is far from a shambles. The town is neatly maintained, and the people, all employees of the Fruit Company and their families, are the most uniformly co-operative one could wish. It is to Mr. John S. Kelley, the manager of the Almirante Division, and his wife, that we chiefly owe the success and pleasure of our collecting in the neighborhood of Almirante, for it was in their home that we made our headquarters. It is largely due to their hospitality that the impedimenta of pressing supplies were conveniently stored away for use, a safe shelter for the presses and kerosene stoves provided, and arrangements made for trips into the surrounding country. From the manner that every need or wish was anticipated, the visiting botanist would seem constantly to have been rubbing the magic lamp of Aladdin.

At the various Fruit Company plantations, appropriately yet unexpectedly, trained and discerning naturalists were much in evidence. Dr. Cordes and Mr. Arnold both are enthusiastic amateur botanists, and both have fine collections of living orchids. At Nievecito, in the valley of the Río Sixaola, we were most fortunate to have Mr. H. J. Bartlet not only as host, but as a guide and companion in the field. Merely following Mr. Bartlet upon his daily travels about the plantation was reward enough for a visit to Panama, because of his activity, understanding, and knowledge of the native vegetation. It was almost in Mr. Bartlet's "front yard" that a very unusual cucurbit was found which it has not been possible to refer satisfactorily to a genus. A most stimulating visit was made

to Mr. J. H. Permar, near Guabito, in the valley of Río Changuinola. We had long been anxious to meet Mr. Permar, since Dr. Popenoe had commented to me, at several times, on his understanding of tropical natural history. Upon his plantation of abacá Mr. Permar has established a small botanical garden of economic plants suitable for cultivation in the tropics of both hemispheres.

Perhaps the most interesting of the trips taken out from Almirante was that arranged for us by Mr. Kelley to the Río Cricamola at the east end of the Chiriquí Lagoon. Leaving Almirante one morning at about four o'clock, we stopped at the town of Bocas del Toro to pick up Mr. H. Wedel, a local ornithologist and accomplished photographer, who was to act as guide and interpreter. Proceeding thence by the United Fruit Company's Diesel-powered yacht "Talamanca," we arrived at the bar of the Río Cricamola shortly before noon. From the bar, we ascended the river in two long *cayucas,* or dug-out canoes, piled high with every convenience which the Fruit Company could provide, including the precaution of six cages of carrier pigeons for communication to Almirante.

We made our headquarters for the several days of our visit, at a ruined plantation called "Finca St. Louis," not far downstream from the Indian village known as Konkintoë. Once an elaborate establishment, the ill-starred Finca St. Louis is a rambling frame building of two stories in a most dismal state of decay. Nothing now remains of the plantings, the lowland jungle pressing close upon every side, as only such tropical second growth can. Upon the rotting fence-posts was found good collecting of many epiphytes ordinarily growing high in trees. Amongst these were some interesting novelties and new records in Orchidaceae and Gesneriaceae. In the half-submerged borders of the river a good representation of Marantaceae, Zingiberaceae, and Araceae was collected. And with the aid of Martin Sparks, a young Bocatoreño who had accompanied us in a duplex rôle of butler and scientific technician, a fair sample was taken of all available flowering and fruiting trees.

After returning again to the comparative luxury of Bocas del Toro, we accepted the hospitality of Mr. Wedel for a collecting trip upon Isla de Colón, where the town of Bocas del Toro is situated. With only a short time at our disposal, scarcely a decent start could be made in the botanical exploration of this interesting and accessible district. But, thanks to the kindly experience of Mr. Wedel, in only a few days numerous additions were made to the known flora of Panama, here very similar to that of Atlantic coastal Costa Rica. There is probably no one in the vicinity of the Chiriquí Lagoon who is quite so familiar with the country and its inhabitants as Mr. Wedel. Since last spring, he has started independently collecting, sending his specimens to the Missouri Botanical Garden for identification and distribution.

LYCOPODIACEAE

(William R. Maxon, Washington, D. C.)

Lycopodium erythraeum Spring—chiriquí: Loma Larga to summit, Volcán de Chiriquí, alt. ca. 3000 m., July 5, 1938, *Woodson, Allen & Seibert 1079.* Previously known only from Ecuador, Peru, and Bolivia. It almost certainly occurs in Colombia as well.

ISOETACEAE

(W. R. Maxon and C. V. Morton, Washington)

Isoetes **panamensis** Maxon & Morton, sp. nov. Sect. *Tuberculatae.* Planta aquatica; rhizoma trilobatum grossum, ca. 3 cm. latum; folia rigida, ca. 50, ca. 32 cm. longa, 2 mm. medio lata, apice acuminata, basi valde dilatata (margine hyalina ca. 8 cm. longa, basi 5–6 mm. lata utroque latere), valde triquetra, septis transversis numerosis perspicuis, stomatibus numerosis, fasciculis fibrovascularibus periphericis validis 6; ligula deltoidea, ca. 3.5 mm. longa, 5 mm. basi lata, acuta; vellum nullum; sporangia magna, ambitu elliptica, ca. 13 mm. longa, 6–7 mm. lata; macrosporae albae, 350–500 μ diam., valide ubique tuberculatae, tuberculis non confluentibus, magnis, elongatis (saepe 25 μ longis), apice rotundatis, costis commissuralibus perspicuis; microsporae parvae, ca. 25 μ diam., laeves.—panamá: pond, vicinity of Bejuco, Aug. 7, 1938.

Woodson, Allen & Seibert 1685 (U. S. Nat. Herb. no. 1,748,502, TYPE).

In Dr. Pfeiffer's monograph the present species seems to be nearest *Isoetes Malinverniana* Cesati & De Not. of Italy. Specimens collected by Cesati and Malinverni and others, kindly lent by the New York Botanical Garden and the Gray Herbarium, show that species to differ in having the ligule lanceolate, the macrospores larger (660–900 μ), and the microspores roughened. *Isoetes cubana* Engelm., of Cuba and British Honduras (?), is a laxer and more slender plant, with macrospores bearing low rounded tubercles. *I. Gardneriana* A. Br. of Brazil is similar in habit, but the macrospores are dark brown and bear fine tubercles.

In the treatment by U. Weber[1] *I. panamensis* would fall in the section *Amphibiae* near *I. Gardneriana* and *I. triangula* Weber. The latter is represented in the U. S. National Herbarium by a specimen of the type collection *(Ule 8000,* from Río Branco, Amazonas, Brazil). It is distinguished from *I. panamensis* by the bilobed rhizome and the small sporangia (5 mm. long).

No species of *Isoetes* has previously been known from Panama, and only one species has been found in adjacent Central America, namely, *I. Storkii* T. C. Palmer, of the mountains of Costa Rica. *Isoetes panamensis* is a lowland species growing near sea level.

HYMENOPHYLLACEAE
(William R. Maxon, Washington, D. C.)

TRICHOMANES ANKERSII Hook. & Grev.—BOCAS DEL TORO: fronds thickly "plastered" to tree trunk, Isla de Colón, alt. ca. 25–75 m., Aug. 18, 1938, *Woodson, Allen & Seibert 1933.* Previously known from Costa Rica, and from Colombia to Bolivia.

POLYPODIACEAE
(William R. Maxon, Washington, D. C.)

DIPLAZIUM LINDBERGII (Mett.) Christ.—BOCAS DEL TORO: vicinity of Nievecito, alt. ca. 15 m., Aug. 8, 1938, *Woodson, Allen*

[1] U. Weber, "Zur Anatomie und Systematik der Gattung Isoetes L.," Hedwigia **63**: 219–262. 1922.

& Seibert 1801. This species, newly recorded from Panama, was described from Brazil, and is reported from Mexico (perhaps in error), Colombia, and Venezuela. At the U.S. National Herbarium we have under this cover specimens ranging from Costa Rica to Colombia and Bolivia. The Panama plant agrees with the Costa Rican specimens, but this material may not be conspecific with the Brazilian type. As regarded at present it must be reckoned a polymorphic species.

Elaphoglossum Dombeyanum (Fée) Moore—chiriquí: steep cliffs of Potrero, near summit, Volcán de Chiriquí, alt. ca. 3300 m., July 5, 1938, *Woodson, Allen & Seibert 1048.* Known previously from Colombia, Venezuela, and Ecuador.

Struthiopteris loxensis (HBK.) Maxon—chiriquí: Loma Larga to summit, Volcán de Chiriquí, alt. ca. 3000 m., July 5, 1938, *Woodson, Allen & Seibert 1067.* Specimens in the U.S. National Herb. are from Colombia, Ecuador, Peru, and Bolivia.

OPHIOGLOSSACEAE

(R. T. Clausen, Ithaca, N. Y.)

Ophioglossum nudicaule L.f. var. tenerum (Mettenius) Clausen—panamá: wet savanna, east of Pacora, June 19, 1938, *Woodson, Allen & Seibert 727.* The first record of this species from Central America.

CYPERACEAE

(H. K. Svenson, Brooklyn, N. Y.)

Carex Lemanniana Boott—chiriquí: common on potrero, forming dense tussocks, near summit, Volcán de Chiriquí, alt. ca. 3300 m., July 4–6, 1938, *Woodson, Allen & Seibert 1057.* Reported by Standley (Fl. Costa Rica 1: 96. 1937) as occurring from Costa Rica to Ecuador at altitudes above 2000 m., but apparently never before collected in Panama.

Cyperus albomarginatus Mart. & Schrad.—canal zone: near Fort Kobe road, July 22, 1938, *Woodson, Allen & Seibert 1427.* Not previously reported from Panama. This number is very peculiar in its light scales; all other material examined from Mexico and Central America has ferruginous scales.

Rynchospora triflora Vahl—panamá: boggy grasslands and marginal thickets between Pacora and Chepo, Aug. 1, 1938, *Woodson, Allen & Seibert 1663.* A widespread tropical species not reported from Central America.

BROMELIACEAE
(L. B. Smith, Cambridge, Mass.)

Tillandsia punctulata Schlechtd. & Cham.—chiriquí: vicinity of Casita Alta, Volcán de Chiriquí, alt. ca. 1500–2000 m., June 28–July 2, 1938, *Woodson, Allen & Seibert 991.* Previously known from southeastern Mexico to Costa Rica, and reported from Surinam.

Vriesia **Woodsoniana** L. B. Smith, spec. nov. (pl. 20), acaulis; foliis rosulatis, ad 5 dm. longis, vaginis ellipticis, basi castaneis, dense punctato-lepidotis, laminis ligulatis, 3 cm. latis, apice rotundato-apiculatis, concoloribus, subtus minute denseque lepidotis, supra glabris; scapo erecto, glabro, vaginis foliaceis dense induto; inflorescentia simplicissima, curvata, subdense pauciflora, ca. 15 cm. longa; bracteis florigeris imbricatis, paulo secunde versis, latissime ovatis, ad apicem versus triangulo-acutis, ad 45 mm. longis et 33 mm. latis, quam sepala longioribus, glabris, valde rugosis, nullo modo carinatis, basi atro-castaneis; floribus valde secundis; pedicellis 1 cm. longis, valde incrassatis; sepalis late ovatis, acutis, 35–40 mm. longis, subtenuibus, impresso-puncticulatis; petalis imperfecte cognitis, basi ligulis binis ad 1 cm. longis auctis; staminibus verisimiliter inclusis.—chiriquí: Bajo Mona, mouth of Quebrada Chiquero, along Río Caldera, alt. ca. 1500–2000 m., July 3, 1938, *Woodson, Allen & Seibert 1029* (Herb. Missouri Bot. Garden, type; Gray Herb., photograph and analytical drawings). In its combination of rugose floral bracts and secund flowers, *Vriesia Woodsoniana* is quite unlike any previously known species.

JUNCACEAE

Luzula gigantea Desv. var. **vulcanica** Woodson, var. nov., a var. typ. differt foliis angustioribus (0.7–0.9 cm. latis) margine longiuscule denseque ciliatis; tepalis saturate castaneis apice

vix mucronulatis.—CHIRIQUÍ: "El Potrero," Volcán de Chiriquí, alt. ca. 3380 m., July 4–6, 1938, *Woodson, Allen & Seibert 1094* (Herb. Missouri Bot. Garden, TYPE). This is apparently the first record of the species from Panama. Only the forbidding technical difficulties of the genus prevent me from describing var. *vulcanica* as a species, so different does it appear, especially in the foliage, from material that I have seen from Mexico and Costa Rica, and from published plates from South American plants. It forms extensive colonies on the volcanic floor of "El Potrero," immediately beneath the peak of the Volcán de Chiriquí.

MUSACEAE

HELICONIA **nutans** Woodson, spec. nov. (Sect. *Taeniostrobus* O.Ktze.). Herba valida ca. 2-metralis. Folia longe petiolata, petioli 25–30 cm. longi subteretes longitudinaliter striati ca. 0.3 cm. crassi, vagina 20 cm. longa ore membranacea purpurissata, lamina oblongo-elliptica apice abrupte acuminata basi late cordata apice obtusa usque 60 cm. longa 24 cm. lata superne minora utrinque viridis glabra. Inflorescentia longe pedunculata, pedunculo 20–32 cm. longo graciliusculo erecto glabro, rhachi nutanti flexuoso-curvato 15–25 cm. longo ca. 0.4 cm. diam. dense ferrugineo-tomentoso, bracteis 4–7 ambitu lanceolatis latiuscule cymbiformibus apice longe acuminatis basi subamplexicaulibus 6–13 cm. longis 2.0–2.5 cm. latis carinatis rubidulis margine extus minute ferrugineo-hirtellis caeterumque glabris, bracteolis ovatis acuminatis 2–4 cm. longis papyraceis nervo medio ferrugineo-hirtellis caeterumque glabris. Flores in bractearum axillis ca. 4–7, pedicellis ca. 0.2 cm. longis sparse pilosulis, ovario clavato ca. 0.6 cm. longo apice ca. 0.25 cm. crasso glabro, tepalis anguste lanceolatis acuminatis ca. 4.7 cm. longis paulo arcuatis aurantiacis extus margine pilosulis intus omnino pilosulis, staminibus 5, filamentis 5 cm. longis tomentellis, antheris haud visis, staminodio vix 0.3 cm. longo, stylo 5 cm. longo glabro. Capsula ovoidea 1 cm. longa 0.8 cm. crassa glabra atro-violacea.—CHIRIQUÍ: vicinity of Casita Alta, Volcán de Chiriquí, alt. 1500–2000 m., June 28–July 2, 1938, *Woodson, Allen & Seibert 968* (Herb. Missouri Bot. Garden, TYPE).

Apparently most closely related to *H. marginata,* of Darién province, Panama, but differing in the cordate leaves and smaller inflorescence, as well as in technical details of the flowers.

ZINGIBERACEAE

COSTUS LIMA K.Sch.—CHIRIQUÍ: moist valley thickets, west of Remedios, June 24, 1938, *Woodson, Allen & Seibert 786;* BOCAS DEL TORO: vicinity of Nievecita, alt. 0–50 m., Aug. 8–19, 1938, *Woodson, Allen & Seibert 1835.* This magnificent species with dark crimson, leafy bracts, which was previously considered as endemic to Costa Rica, was found in numerous localities at low elevations upon both coasts of Panama in Chiriquí and Bocas del Toro. One variation of the species from the latter province, which is distinguished well by its pale pink or flesh-colored bracts, may be described as follows:

COSTUS LIMA K.Sch. var. **Wedelianus** Woodson, var. nov., ab var. typ. bracteis obtusiusculis brevioribus carneisque differt. —BOCAS DEL TORO: Río Cricamola, between Finca St. Louis and Konkintoë, alt. ca. 10–50 m., Aug. 12–16, 1938, *Woodson, Allen & Seibert 1926* (Herb. Missouri Bot. Garden, TYPE). This variety, which may well merit specific rank, is named in honor of Mr. H. Wedel, the ornithologist of the city of Bocas del Toro, to whom we owe much aid during the trip up the Cricamola River and elsewhere in Bocas del Toro.

COSTUS ARGENTEUS R. & P.—PANAMÁ: thickets and forests near Arraiján, alt. ca. 15 m., July 21, 1938, *Woodson, Allen & Seibert 1358;* CHIRIQUÍ: thickets west of Remedios, June 24, 1938, *Woodson, Allen & Seibert 789.* Considerable confusion has surrounded the identity of this magnificent species, which is common in midsummer in the Canal Zone and occurs elsewhere in the Republic upon both coasts, especially the Pacific. Recorded distribution of *C. argenteus* has been confined to western Peru and Ecuador. All the collections of the species that I have seen have been assigned to *C. villosissimus* Jacq., a very different and common plant of smaller stature and covered everywhere save the flower itself with a long, yellow-hirsute indument. Plate 14 in Standley's "Flora of the Panama

Canal Zone," represents *C. argenteus* rather than *C. villosissimus.* The two species, occurring so commonly together, present strong evidence of hybridization. *Seibert 593,* collected in the vicinity of Gold Creek, near Gamboa, Canal Zone, and distributed as *C. villosissimus,* is a striking example of the putative hybrids.

Recently I have had the good fortune, through the kindness of Professor Domin, of examining the type of *C. hirsutus* Presl (*Haenke s.n.* in Herb. Mus. Nat. Prag.). The specimen appears to me quite conspecific with those more correctly referred to *C. villosissimus* Jacq.

Renealmia exaltata L.f.—bocas del toro: Río Cricamola, between Finca St. Louis and Konkintoë, alt. ca. 10–50 m., Aug. 12–16, 1938, *Woodson, Allen & Seibert 1905.* It is almost incredible that this common and widespread species of the Caribbean and northeastern South America has not previously been reported for Panama. Neither have I seen herbarium specimens from the republic. It is not uncommon in the lowlands bordering the Río Cricamola, and probably is to be found elsewhere along the Atlantic coast.

MARANTACEAE

Calathea **quadratispica** Woodson, spec. nov. Planta valida 2–3 m. alta. Folia longissime petiolata, petioli pars superior paulo compressa callosa 15–17 cm. longa glabra vel minutissime sparseque papillosa pars inferior ca. 75–95 cm. longa, lamina inaequilateraliter ovata basi late obtusa apice rotundata 80–95 cm. longa 47–50 cm. lata utrinque viridis inferne paulo pallidior durius herbacea margine minute puberula caeterumque glabra, vagina scariacea 25–26 cm. longa margine minute puberula. Spicae 2 quadrato-cylindricae 14–15 cm. longae ca. 3 cm. diam., pedunculo 25–30 cm. longo apice dense puberulo in vagina incluso; bracteae distichae 30–34 dense imbricatae latissime ovatae vel suborbiculatae apice rotundatae vel paululo retusae margine vulgo plus minusve revolutae ad 3 cm. longae sparse minuteque pilosulae superne apicem versus densius scariaceae aureae 6–8-florae; paria

florum brevissime (ca. 0.1 cm. vel minus) pedicellatorum 8–12 bracteolis scariaceis exterioribus ca. 2.5 cm. longis ca. 1.2 cm. latis latissime oblongis valde conduplicatis apice truncatis haud profunde 2–4-lobatis interioribus multo minoribus oblongo-lanceolatis acuminatis; ovarium ca. 0.3 cm. longum glabrum vel minute papillatum; sepala oblonga late obtusa 1.7–1.8 cm. longa glabra; corollae flavae tubus anguste cyatho-cylindricus 2.8–3.0 cm. longus basi ca. 0.07 cm. diam., ostio ca. 0.125 cm. diam., lobi ovato-lanceolati acuti ca. 0.8 cm. longi, stamen paululo exsertum 0.3 cm. longum compresse ellipsoideum, staminodium exterius oblique obovatum flavum 1.1 cm. longum, callosum brevius cucullatum 0.7 cm. longum; capsula non visa.—BOCAS DEL TORO: swampy margins of Río Cricamola, between Finca St. Louis and Konkintoë, Aug. 12–16, 1938, *Woodson, Allen & Seibert 1913* (Herb. Missouri Bot. Garden, TYPE). When first studied, this species was thought possibly to represent *C. sclerobractea* K.Sch., which is known to occur only in Guatemala. From the latter, however, and from all other species known to me, *C. quadratispica* differs quite obviously in the rather strongly quadrate-compressed spikes. It is not uncommon in the valley of the Río Cricamola, where it occurs with the familiar *C. lutea* and *C. insignis.*

ORCHIDACEAE

(L. O. Williams, Cambridge, Mass.)

PHRAGMIPEDIUM CAUDATUM (Lindl.) Rolfe, in Orch. Rev. **4**: 332. 1896; Pfitzer, in Engl. Pflanzenr. **IV**. 50 (Heft 12): 52. 1903, in synon.—*Cypripedium caudatum* Lindl., Gen. & Sp. Orch. Pl. 531. 1840; *Selinipedium caudatum* Rchb.f., in Bonplandia **2**: 116. 1854; *Paphiopedilum caudatum* Pfitzer, in Engl. Bot. Jahrb. **19**: 41. 1894; *Paphiopedium caudatum* Kerch., Orch. 454. 1894.—CHIRIQUÍ: vicinity of Casita Alta, alt. 1500–2000 m., June 28–July 2, 1938, *Woodson, Allen & Seibert 962.*

Phragmipedium caudatum has been reported from Chiriquí by Reichenbach (Beitr. Orch. Centr.-Am. 44. 1867), but no specimen was cited by him. The specimen cited above would

seem to be the second collection from Panama. The species is known in Costa Rica, Colombia, Ecuador, and Peru.

The original spelling of the generic name was *Phragmipedium.* Pfitzer changed the spelling to *Phragmopedilum,* in his treatment of the group, and accredited all the combinations to Rolfe except one.[1] This change of the spelling of the generic name is not permissible.

Habenaria heptadactyla Rchb.f., in Linnaea **22**: 812. 1849. —panamá: terrestrial, thickets and forests near Arraiján, alt. about 15 m., July 21, 1938, *Woodson, Allen & Seibert 1406;* without definite locality (Canal Zone or Panama Province), *A. M. Bouché, Jr. 7.*

Habenaria heptadactyla does not seem to have been reported from Panama previously. It is known to occur in Venezuela, British Guiana, and Brazil.

Habenaria pauciflora (Lindl.) Rchb.f., in Bonplandia **2**: 10. 1854.—*Habenaria setifera* Lindl., in Ann. Nat. Hist. **4**: 381. 1840.—panamá: boggy grasslands and marginal thickets, between Pacora and Chepo, alt. about 25 m., Aug. 1, 1938, *Woodson, Allen & Seibert 1665.*

Previously reported from Chiriquí as *H. setifera* by Schweinfurth (Ann. Mo. Bot. Gard. **24**: 182. 1937). This species ranges from Mexico to Argentina.

Ponthieva Ephippium Rchb.f., in Linnaea **28**: 382. 1856.—chiriquí: terrestrial, Finca Lérida to Boquete, alt. 1300–1700 m., July 8–10, 1938, *Woodson, Allen & Seibert 1118.*

New to Panama and Central America. Not previously recorded south of the state of Puebla in Mexico.

Ponthieva Ephippium is very closely allied to *P. racemosa* (Walt.) Mohr, but has a lip with two small calluses at the base of the blade and is usually a smaller plant with smaller flowers.

Pleurothallis vittata Lindl., in Bot. Reg. **24**: Misc. 73. 1838; Fol. Orch. Pleurothallis, 18. 1859.—*Pleurothallis poly-*

[1] Phragmipedium **Hartwegii** (Rchb.f.) L. O. Williams, comb. nov.—*Cypripedium Hartwegii* Rchb.f., in Bot. Zeit. **10**: 714. 765. 1852; *Selinipedium Hartwegii* Rchb.f., in Bonplandia **2**: 116. 1854; Xen. Orch. **1**: 3, 70. *t.27.* 1854; *Phragmopedilum Hartwegii* Pfitzer, in Engl. Pflanzenr. **IV.** 50 (Heft 12): 48. 1903.

stachya Rich. & Gal., in Ann. Sci. Nat. III, **3:** 16. 1845; *Pleurothallis mandibularis* Kränzl., in Vid. Medd. Naturh. Foren. **71:** 169. 1920; *Pleurothallis Bourgeaui* Kränzl., in Ark. f. Bot. **16**[8]: 15. 1920.—COCLÉ: epiphytic, between Las Margaritas and El Valle, July 15–Aug. 8, 1938, *Woodson, Allen & Seibert 1282.*

Pleurothallis vittata is new to the flora of Panama. Previously it has been known from Mexico and Honduras and was reported from Venezuela by Lindley. The record for Venezuela cannot be verified here, as the specimen on which the record was based *(Fendler 1481)* is lacking from the Fendler collection at the Gray Herbarium.

MALAXIS MAJANTHEMIFOLIA Schltr. & Cham., in Linnaea **6:** 59. 1831.—CHIRIQUÍ: terrestrial, vic. of Casita Alta, Volcán de Chiriquí, alt. 1500–2000 m., June 28–July 2, 1938, *Woodson, Allen & Seibert 830.*

Malaxis Majanthemifolia is new to the flora of Panama. The species was previously recorded from Mexico, Honduras, and Guatemala. The flowers of the Panamanian collection are somewhat unusual in that the lateral sepals are adnate almost to their tips.

MALAXIS PARTHONII Morren, in Bull. Acad. Roy. Belg. **5:** 485, *t.* 1838.—CHIRIQUÍ: terrestrial, Finca Lérida to Boquete, alt. 1300–1700 m., July 8–10, 1938, *Woodson, Allen & Seibert 1172;* CANAL ZONE: terrestrial, vic. of Salamanca Hydrographic Station, Río Pequení, alt. about 80 m., July 28–29, 1938, *Woodson, Allen & Seibert 1581.*

Malaxis Parthonii seems not to be recorded from Panama although it is known from Mexico to Costa Rica and again in northern South America.

MALAXIS **Woodsonii** L. O. Williams, sp. nov. (pl. 21, figs. 1–2). Herba nana, terrestris. Caulis brevis, inferne bulbosus, supra medium bifoliatus. Folia subaequalia, late ovata. Inflorescentia subumbelliformis. Segmenta perianthii patentia. Sepala late lanceolata, obtusa. Petala filiformia. Labellum quadratum, apice trilobatum; auriculae lineari-lanceolatae, acutae. Columna minuta.

Small terrestrial herbs up to about 15 cm. tall. Stems short,

swollen and pseudobulbous below, covered with the sheathing petioles of the leaves and by basal bracts. Leaves two, subequal, broadly ovate, obtuse or acute, 1.5–5.5 cm. long and 1.3–4.5 cm. broad, appearing sessile and to be borne well above the middle of the stem but actually with a long petiole which sheathes the stem, margin of the blade crenulate or obscurely serrate, several-nerved. Inflorescence many-flowered; floral bracts short, lanceolate, scarious; pedicels erect or spreading, about 1 cm. long. Sepals broadly lanceolate, obtuse, obscurely 3-nerved, 2.5–4 mm. long and 1.5–2.5 mm. broad, margins strongly recurved, especially on the dorsal sepal. Petals filiform, about 2.5–3 mm. long. Lip quadrate in outline, about 3.5–5 mm. long and 3–3.5 mm. broad; apex of the lip 3-lobed, mid-lobe small, exceeded by the lateral lobes in length, lateral lobes large, rounded, obtuse; the basal auricles linear-lanceolate, acute, 1–2 mm. long, parallel to the axis of the lip, arising well up from the base of the lip; disk with two shallow cavities extending from the base of the column. Column short, about 1 mm. long.—CHIRIQUÍ: terrestrial, vic. of Casita Alta, Volcán de Chiriquí, alt. about 1500–2000 m., June 28–July 2, 1938, *Woodson, Allen & Seibert 831* and *832* (Herb. Ames, Cambridge, Mass., No. 55,715, TYPE).

Malaxis Woodsonii is distinguished from all other American species by the position of the basal auricles of the lip as well as by less obvious characters.

LIPARIS ELATA Lindl., in Bot. Reg. **14**: *t. 1175*. 1828.—CANAL ZONE: epiphytic, vic. of the Salamanca Hydrographic Station, Río Pequení, alt. about 80 m., July 28–29, 1938, *Woodson, Allen & Seibert 1580*.

Although *Liparis elata* does not seem to have been recorded from Panama previously it ranges from Florida, the West Indies, and Mexico, south to northern South America.

EPIDENDRUM **Boothii** (Lindl.) L. O. Williams, comb. nov.—*Maxillaria Boothii* Lindl., in Bot. Reg. **24**: Misc. 52. 1838; *Dinema paleaceum* Lindl., in Bot. Reg. **26**: Misc. 51. 1840; *Epidendrum auritum* Lindl., in Bot. Reg. **29**: Misc. 4. 1843; *Epi-*

dendrum Lindenianum Rich. & Gal., in Ann. Sci. Nat. III, **3**: 20. 1845; *Epidendrum paleaceum* Rchb.f., Beitr. Orch. Centr.-Am. 80. 1860; in Saunders' Ref. Bot. **2**: *t. 87.* 1869; Ames, Hubbard & Schweinf., Genus Epidendrum in U. S. & Mid. Am. 140. 1936; *Nidema Boothii* Schltr., in Fedde Repert. Beih. **17**: 43. 1922.—BOCAS DEL TORO: epiphytic, Río Cricamola, between Finca St. Louis and Konkintoë, alt. about 10–50 m., Aug. 12–16, 1938, *Woodson, Allen & Seibert 1892.*

Epidendrum Boothii is new to the flora of Panama, although it was known in Mexico, throughout Central America except Panama, Cuba, Venezuela and Dutch Guiana.

Ames, Hubbard and Schweinfurth, in their study of *Epidendrum,* did not take up *Maxillaria Boothii,* which is the oldest name for the species, because they supposed that *Epidendrum Boothianum* Lindl. would make a homonym of the combination *Epidendrum Boothii.* This, however, is not the case as *Epidendrum Boothianum* is adjectival in form while *Epidendrum Boothii* is genitive (cf. International Rules of Botanical Nomenclature, ed. 1935, Art. 70, note 4).

EPIDENDRUM ISOMERUM Schltr., in Fedde Repert. **2**: 132. 1906.—BOCAS DEL TORO: epiphytic, pendulous in dense clumps, Río Cricamola, between Finca St. Louis and Konkintoë, alt. about 10–50 m., Aug. 12–16, 1938, *Woodson, Allen & Seibert 1886.*

Epidendrum isomerum does not seem to have been previously reported from Panama, although there is a fragment in the Ames Herbarium collected by G. S. Miller, Jr., near Río Medio in the Canal Zone. Previously recorded from Mexico, Guatemala, Honduras, and Costa Rica.

EPIDENDRUM PRISMATOCARPUM Rchb.f., in Bot. Zeit. **10**: 729. 1852.—CHIRIQUÍ: on fallen logs, Finca Lérida to Boquete, alt. about 1300–1700 m., July 8–10, 1938, *Woodson, Allen & Seibert 1117.*

The type of *Epidendrum prismatocarpum* came from Chiriquí, but there is no record in the Ames Herbarium of the plant having been re-collected in Panama. The species is not uncommon in Costa Rica.

GALEANDRA BAUERI Lindl. in Bauer, Ill. Orch. Pl. Gen. *t. 8.* 1832 (?); Gen. & Sp. Orch. Pl. 187. 1833; in Bot. Reg. **26:** *t. 49.* 1840; Bateman, Orch. Mex. & Guat. *t. 19.* 1840.—*Galeandra Batemanii* Rolfe, in Gard. Chron. III, **12:** 431. 1892.—BOCAS DEL TORO: in swamp near Almirante, at sea-level, flowered in Panama Aug. 20, 1939, (comm. Paul H. Allen to) *Hugo Nash 1962.*

Galeandra Baueri is new to the flora of Panama. It has been recorded previously from Mexico, British Honduras, Guatemala, Honduras, and French Guiana.

Since Rolfe gave a new name to the Mexican plants in 1892, the name seems to have been universally adopted. Rolfe distinguished *G. Batemanii* as having "a short ovoid pseudobulb, and a dull purple lip" and *G. Baueri* as having "a slender fusiform pseudobulb, and a pale-coloured lip." Most of the Mexican and British Honduran material examined has slender pseudobulbs, but the shape seems to depend on age, the younger ones being slender, the older ones thicker. In regard to the coloration of the flowers it must be remembered that Bauer's drawings were made from a dried specimen which could have lost its color—as have most of the specimens in the Ames Herbarium.

WARREA COSTARICENSIS Schltr., in Fedde Repert. **16: 446.** 1920.—CHIRIQUÍ: terrestrial, deep shade near Potrerillos, 1939, *Allen s.n.;* locality lacking, alt. 3000 ft., 1938, *Kieswetter s.n.*

It is with some hesitation that the above plants are referred to Schlechter's species but it is perhaps best to place them here until the species is better known.

In the specimens cited the lip is oval to round and apparently not emarginate, while Schlechter described and drew the lip of *Warrea costaricensis* as oblong and emarginate. If Schlechter's drawings are correct, there are also differences in the stipe and the gland of the pollinia between the Panamanian plants and Schlechter's specimens, which were from Costa Rica.

GOVENIA CILIILABIA Ames & Schweinf., in Sched. Orch. **10**: 80. 1930.—CHIRIQUÍ: vic. of Casita Alta, Volcán de Chiriquí, alt. about 1500–2000 m., June 28–July 2, 1938, *Woodson, Allen & Seibert 947.*

Govenia ciliilabia is the rarest species of the genus in Central America. The original and, until now, the only known specimen of the species was collected at Cola de Galla, Costa Rica.

MAXILLARIA RINGENS Rchb.f., in Walp. Ann. **6**: 523. 1863; C. Schweinf., in Bot. Mus. Leafl. Harv. Univ. **4**: 91. 1937.—CHIRIQUÍ: epiphytic, Bajo Mono, mouth of Quebrada Chiquera, along Río Caldera, alt. about 1500–2000 m., July 3, 1938, *Woodson, Allen & Seibert 1010.*

The collection cited above is rather unusual in the large size of the flowers, otherwise it would seem to be quite typical of the species. The sepals are from 5 to 6 cm. long, and the petals are about 4.5 cm. long.

Known previously from Panama; also from Guatemala, Nicaragua, and Costa Rica. The synonyms, *Maxillaria Rousseauae* Schlecht. and *M. pubilabia* Schlecht., were based on Panamanian material.

RODRIGUEZIA COMPACTA Schltr., in Fedde Repert. Beih. **19**: 144. 1923.—BOCAS DEL TORO: epiphytic, Río Cricamola, between Finca St. Louis and Konkintoë, alt. about 10–15 m., Aug. 12–16, 1938, *Woodson, Allen & Seibert 1888.*

New to Panama. The specimen is past flower but there is little doubt concerning the identity of the plant. Previously recorded from Costa Rica.

OSMOGLOSSUM ANCEPS Schltr., in Fedde Repert. Beih. **19**: 147. 1923.—CHIRIQUÍ: epiphytic, vic. of Casita Alta, Volcán de Chiriquí, alt. about 1500–2000 m., June 28–July 2, 1938, *Woodson, Allen & Seibert 875.*

Previously recorded only from Costa Rica.

ODONTOGLOSSUM OERSTEDII Rchb.f., in Bonplandia **3**: 214. 1855; Xen. Orch. **1**: 189, *t. 68, I.* 1856.—CHIRIQUÍ: epiphytic on dead logs in dense wet forest, Loma Larga to summit, Volcán de Chiriquí, July 4–6, 1938, *Woodson, Allen & Seibert 1030.*

A handsome small plant previously known only from Costa Rica.

NOTYLIA **Cordesii** L. O. Williams, sp. nov. (pl. 21, figs. 3–4). Herba epiphytica, parva. Folia aequantia, lineari-lanceolata vel lanceolata, acuta vel acuminata. Pseudobulbus parvus, complanatus, unifoliatus. Inflorescentia subumbellata; bracteae scariosae, lanceolatae, acutae vel acuminatae. Sepalum dorsale lineari-lanceolatum, acuminatum, trinervium. Sepala lateralia linearia, acuminata, uni- vel binervia. Petala sepalo dorsali similia sed angustiora, basi trinervia. Labellum unguiculatum; unguis medio biauriculatus; lamina hastata, acuminata; lobi laterales recurvi, serrulati. Columna generis.

A small epiphytic herb. Leaves equitant, laterally flattened, linear-lanceolate to lanceolate, acute or acuminate, sessile, 4–6 cm. long, 3–5 mm. broad (laterally). Pseudobulbs small, complanate, inclosed in the bases of leaves, unifoliolate, 1–1.5 cm. long. Inflorescence a subumbellate raceme, simple or branched; scape from the base of a pseudobulb, slender, about 4–6 cm. long, with several infundibuliform bracts; bracts of the inflorescence scarious, lanceolate, acute or acuminate, about 1.5–2 mm. long, spreading. Pedicels filiform, spreading, with the ovary about 6 mm. long. Dorsal sepal linear-lanceolate, acuminate, 3-nerved, about 10 mm. long and 1.5 mm. broad. Lateral sepals linear, acuminate, slightly oblique, 1–2-nerved, about 12–13 mm. long and 1 mm. broad. Petals similar to the dorsal sepal but slightly narrower, 3-nerved at the base, 1-nerved above. Lip arising at the base of the column but free from it, long-unguiculate, the claw about 4 mm. long, thickened and biauriculate at a point half way between the base of the lip and the lateral lobes, the thickening papillose-pubescent on the anterior side; blade of the lip hastate, acuminate, about 4 mm. long and 2 mm. broad, the lateral lobes recurved, serrulate, the apex strongly acuminate. Column slender, about 3 mm. long, characteristic of the genus.—BOCAS DEL TORO: epiphytic, Mosquito Hill, Aug. 12–16, 1938, (comm. by Dr. H. Cordes to) *Woodson, Allen & Seibert 1932* (Herb. Missouri Bot. Garden, TYPE).

Notylia Cordesii is allied to several of the Central American species of the genus, among them *N. bicolor* Lindl., *N. linearis* A. & S., *N. ramonensis* Schltr., and *N. Wullschlaegeliana* Rchb.f. It is most closely allied to the last of these, *N. Wullschlaegeliana,* from which it may be distinguished as a larger plant with distinctly larger leaves and flowers; by having the lip entirely free from the column; by having the auricles near the middle of the claw instead of at the base.

It is a pleasure to name this fine little orchid for Dr. Cordes, who has shown much interest in the flora of Panama.

Telipogon ampliflorus C. Schweinf., in Bot. Mus. Leafl. Harv. Univ. 6: 34. 1938.—chiriquí: epiphyte, vic. of Casita Alta, Volcán de Chiriquí, alt. about 1500–2000 m., June 28–July 2, 1938, *Woodson, Allen & Seibert 961.*

Telipogon ampliflorus, which was recently described from Costa Rica, is new to the flora of Panama. The flowers of the present specimens are somewhat smaller than those described by Schweinfurth.

ROSACEAE

(Alchemilla by L. M. Perry, Jamaica Plain, Mass.)

Alchemilla pectinata HBK.—chiriquí: vicinity of Casita Alta, Volcán de Chiriquí, alt. 1500–2000 m., common in clearings, June 30, 1938, *Woodson, Allen & Seibert 892;* Loma Larga to summit, Volcán de Chiriquí, alt. 2500–3380 m., July 5, 1938, *Woodson, Allen & Seibert 1042.* Known to extend from Mexico to Colombia and Bolivia, but previously unknown from Panama. No. *1042* is a typical specimen; *892* is a more stoloniferous and smallish specimen, but apparently belongs to this species.

Alchemilla aphanoides L.f. var. subalpestris (Rose) Perry—chiriquí: Loma Larga to summit, Volcán de Chiriquí, alt. 2500–3380 m., July 5, 1938, *Woodson, Allen & Seibert 1041.* Originally described from Mexico. I have not seen previously this plant from farther south than Costa Rica. Reported by Standley (Fl. Costa Rica 2: 477. 1937) as extending to Bolivia.

Hesperomeles **chiriquensis** Woodson, spec. nov. Arbuscula dense ramosa 1.5–3.0 dm. alta; ramis sat crassis subfastigiatis; ramulis juventate dense minuteque fulvo-hispidulis mox glabratis haud spinescentibus, internodiis 0.1–0.4 cm. longis; foliis plerumque obovato-suborbicularibus apice rotundatis vel paulo retusis rare subacutis basi late cuneatis 0.3–2.0 cm. longis 0.2–1.9 cm. latis margine inconspicue depresso-serrulatis coriaceis supra paulo illustris nervo medio dense minuteque fulvo-hispidulis subtus pallidioribus opacis nervo medio sparse hispidulis caeterumque glabris; petiolo 0.2 cm. longo fulvo-hispidulo; inflorescentiis corymbosis densis plurifloris; bracteis subfoliaceis lanceolatis 0.4–0.8 cm. longis; pedicellis subnullis; cupulis late conicis 0.3 cm. longis 0.35 cm. latis extus fulvo-hispidulis intus dense villosulis; sepalis triangulo-setosis 0.35 cm. longis ut in cupula vestitis; petalis obovato-oblongis 0.5 cm. longis 0.4 cm. latis basi unguiculatis pallide roseis; staminibus 20, filamentis 0.15–0.3 cm. longis, antheris 0.07 cm. longis; pistillis 0.5 cm. longis basi villosulis; fructu ignoto.—chiriquí: Loma Larga to summit, Volcán de Chiriquí, alt. ca. 3300 m., July 4–6, 1938, *Woodson, Allen & Seibert 1078* (Herb. Missouri Bot. Garden, type).

This handsome dwarf tree was found almost literally covered with its pale pink flowers, not far below the summit of the volcano. *H. obovata* (Pittier) Standl., of the neighboring peaks of Costa Rica, is distinguished from it by its white, smaller petals, and spinescent twigs. The extremely dwarf stature and very crowded foliage, probably induced by the high altitude, are also distinctive, as well as the depressed serrulation of the leaves.

POLYGALACEAE

(S. F. Blake, Washington)

Monnina xalapensis HBK.—chiriquí: vicinity of Casita Alta, Volcán de Chiriquí, alt. 1500–2000 m., June 28–July 2, 1938, *Woodson, Allen & Seibert 802.* Apparently new to Panama; previously known from Vera Cruz to Nicaragua and Costa Rica.

EUPHORBIACEAE

(P. C. Standley, Chicago)

CROTON **Allenii** Standl., sp. nov. Arbuscula 4-metralis ramosa, ramis gracilibus teretibus ochraceis sparse pilis stellatis sessilibus pauciradiatis pilosis, sat dense foliatis, internodiis brevibus vel elongatis; stipulae filiformi-subulatae 1.5–2 mm. longae apice glanduliferae deciduae; folia inter minora longipetiolata herbacea, petiolo gracili 2–3.5 cm. longo sparse stellato-piloso; lamina ovata vel oblongo-ovata 5–8 cm. longa 2.5–4.5 cm. lata acuta vel subabrupte breviter acuminata, basi late rotundata atque breviter cordata, arcte crenato-serrulata, utrinque viridis, sparsissime praesertim ad nervos stellato-pilosa, e basi 5-nervia, nervo medio supra basin utroque latere nervos ca. 4 emittente; flores monoeci racemosi, racemis terminalibus breviter pedunculatis 4–7 cm. longis laxe remotifloris, rhachi sat dense stellato-pilosa, pedicellis 1–3 mm. longis; flores fertiles pauci vulgo 1–2, interdum usque 6, sepalis 5 in statu fructifero 5–6 mm. longis subaequalibus lanceolato-oblongis acutis remote serratis dense stellato-pilosis erectis, petalis nullis; styli bis dichotome divisi glabri; flores masculi numerosi cito decidui in alabastro globosi atque 2.5 mm. diam., sparse stellato-pilosi; stamina ca. 10, filamentis glabris; capsula vix matura 5 mm. longa ubique dense pilis parvis patentibus stellato-pilosa.—COCLÉ: vicinity of Antón, Aug. 8, 1938, *Woodson, Allen & Seibert 1711* (Herb. Field Mus., TYPE; duplicate in Herb. Missouri Bot. Garden).

A notable addition to the rather few species of *Croton* known from Panama, distinctive in appearance because of its rather small and bright green leaves, which at first sight appear to be glabrous. The hairs of the pubescence vary considerably in form, but many of them are distinguished by having short basal rays and very long and soft central ones.

PLUKENETIA VOLUBILIS L.—LOS SANTOS: thickets between Los Santos and Guararé, July 11, 1938, *Woodson, Allen & Seibert 1201.* Apparently known from Central America only by this specimen. It is recorded or represented also from Dominica,

Colombia, Peru, and Bolivia. At least one other species of the genus occurs in northern Central America.

DILLENIACEAE

(P. C. Standley, Chicago)

Saurauia **Seibertii** Standley, sp. nov. Arbor, ramulis crassiusculis fere glabris sed sparsissime atque fere minute adpresso-furfuraceis; folia petiolata crassiuscula atque in sicco rigidula, petiolo 1.5–3.5 cm. longo sparse adpresso-furfuraceo; lamina oblongo-lanceolata 15–20 cm. longa 4.5–5.5 cm. lata acuminata, basin acutam versus paullo angustata, in toto margine arcte serrata, supra sublucida glaberrima, subtus ad nervos sparsissime adpresso-furfuracea, costa crassiuscula elevata, nervis lateralibus utroque latere ca. 15 angulo semirecto vel paullo latiore adscendentibus prominentibus teneris; paniculae axillares longipedunculatae folia aequantes vel paullo longiores, pedunculo usque 15 cm. longo minute sparse tomentello atque sparse adpresso-furfuraceo, paniculis amplis sublaxe multifloris ca. 12 cm. longis atque aequilatis, ramis dense tomentellis et sparse breviter furfuraceis, bracteis conspicuis interdum foliaceis angustis, pedicellis gracilibus dense tomentellis usque 15 mm. longis; sepala rotundato-ovata vel late elliptica ca. 8 mm. longa apice obtusa vel rotundata, utrinque densissime minute tomentella; petala alba glabra rotundato-elliptica vel ovalia ca. 14 mm. longa—chiriquí: Bajo Mono, mouth of Quebrada Chiquero, along Río Caldera, alt. 1500–2000 m., "common along Río Caldera," July 3, 1938, *Woodson, Allen & Seibert 1020* (Herb. Field Mus., type; duplicate in Herb. Missouri Bot. Garden).

The practically glabrous, rather coarsely and regularly serrate leaves of this plant isolate it among the various Panama species of *Saurauia*. It is not closely similar to any of the rather numerous species occurring in Costa Rica.

TILIACEAE

Luehea candida (Moc. & Sessé) Mart.—coclé: llanos between Aguadulce and Antón, alt. ca. 15–50 m., July 12, 1938, *Woodson, Allen & Seibert 1203.* A handsome tree 10–15 m.

tall, bearing showy, white flowers. Not infrequent in the locality visited, but apparently not previously reported from Panama.

BUXACEAE

(C. L. Lundell, Ann Arbor, Mich.)

Buxus citrifolia Spreng.—canal zone: vicinity of Salamanca Hydrographic Station, Río Pequení, alt. ca. 80 m., July 28–29, 1938, *Woodson, Allen & Seibert 1563.* This interesting shrub has not been known previously to occur in Central America, having been collected or reported only in Cuba, Puerto Rico, and Venezuela.

CELASTRACEAE

(C. L. Lundell, Ann Arbor, Mich.)

Maytenus **Woodsoni** Lundell, sp. nov. (pl. 22). Arbor 3 m. alta. Ramuli verticillati, breves et crassiusculi, striati, glabri. Folia glabra, coriacea, obovata, oblanceolata, oblanceolato-oblonga vel elliptica, 4–8 cm. longa, 1.8–4.1 cm. lata, vel interdum minora, apice acuta, obtusa vel rotundata, basi late cuneata, revoluta, supra mediam serrulata, venis utrinque 6 vel 7, reticulatis; petiolis 3–5 mm. longis. Flores fasciculati. Pedicelli usque ad 5 mm. longi, glabri. Calyx quinquefidus, lobis laciniatis, late ovatis vel suborbicularibus, 1.2–1.8 mm. longis, glabris. Petala vinacea, late ovata vel suborbicularia, usque ad 2.5 mm. longa, erosa. Stamina 5. Ovarium 3-loculare, ovulis in loculis solitariis. Pedicelli fructiferi 3.5–6 mm. longi. Capsula late obovoidea, 6–7 mm. longa. Semina 1 vel 3, arillata, obovoidea, ca. 4.5 mm. longa.

A tree 3 m. high; branchlets verticillate, rather short and stout, striate and angled, glabrous; buds covered with rufous-laciniate scales. Leaves glabrous, subverticillate at apex of branchlets, alternate otherwise. Stipules ligulate, up to 2.5 mm. long, maroon, long-laciniate. Petioles stout, 3 to 5 mm. long, shallowly grooved above. Leaf blades coriaceous to rigidly coriaceous, obovate, oblanceolate, oblanceolate-oblong or elliptic, usually 4 to 8 cm. long, 1.8 to 4.1 cm. wide, sometimes smaller, apex acute to rounded, base broadly cuneate, margin slightly revolute, conspicuously serrulate above the middle,

the serratures rounded and apiculate with short red inflexed teeth, costa prominent and rather thick beneath at base, slender toward apex, slightly elevated above, main lateral veins 6 or 7 on each side, prominulous beneath, plane or slightly impressed above, veinlets reticulate and prominulous beneath. Inflorescence usually at leafless nodes, reduced to a fascicle, the bracteoles of the reduced inflorescence persistent at base of pedicels, maroon, lacinate, forming a compact protuberance. Pedicels up to 5 mm. long, glabrous. Calyx deeply 5-lobed, the lobes red, laciniate, broadly ovate or suborbicular, 1.2 to 1.8 mm. long including fringe, glabrous. Petals vinaceous, broadly ovate or suborbicular, up to 2.5 mm. long, margin erose and colorless. Stamens 5. Ovary 3-celled, with 1 erect ovule in each cell. Fruiting pedicels 3.5 to 6 mm. long, jointed near base. Capsules broadly obovoid, 6 to 7 mm. long, 3-celled, 1- to 3-seeded. Seed arillate, obovoid, about 4.5 mm. long; endosperm copious; cotyledons 2.7 mm. long; radicle stout, terete, about 1 mm. long.—CHIRIQUÍ: Loma Larga to summit, Volcán de Chiriquí, alt. 2500–3380 m., July 4–6, 1938, *Woodson, Allen & Seibert 1065* (Herb. Univ. Michigan, TYPE in flower); same locality, *Woodson, Allen & Seibert 1088* (Herb. Univ. Michigan, COTYPE, in fruit).

M. Woodsoni approaches *M. verticillata* (R. & P.) DC., a species of Peru with varieties in Ecuador and Colombia. The Panama tree may be distinguished by its conspicuously serrulate leaves, fascicled flowers, much larger maroon calyx-lobes, and vinaceous petals. The laciniate margin of the stipules, bracts, and calyx-lobes is a noteworthy characteristic shared apparently by *M. verticillata.* The flowers appear to be dioecious, but from the material available I have not been able to determine this point definitely.

MYRSINACEAE

(C. L. Lundell, Ann Arbor, Mich.)

PARATHESIS **Seibertii** Lundell, sp. nov. Arbor 4–6 m. alta. Ramuli crassiusculi, minute et parce adpresse rufo-lepidoti. Folia anguste oblonga vel oblongo-elliptica, 8.5–19 cm. longa, 2.2–4.6 cm. lata, apice basique acuminata, margine subrepanda

vel integra, membranacea, supra glabra, subtus parce et minute lepidota, nervis patentibus, fere 18-jugis, prominulis, punctulis multis (pleris breviter lineiformibus) auctis; petiolis 1.5–2.5 cm. longis. Inflorescentiae axillares, multiflorae, paniculatae, thyrsoideae, 8–9 cm. longae, parce lepidotae vel glabrae, pedicellis usque ad 6.5 mm. longis, quam bracteis multo longioribus; flores ante anthesin ca. 5 mm. longi, minute rufopuberuli; sepala basi coalita, anguste triangularia, ca. 0.9 mm. longa, punctata; petala intus tomentosa, anguste lanceolato-attenuata, 5 mm. longa, basi coalita, punctata; stamina 3–3.2 mm. longa, antheris apiculatis, 1.7–2 mm. longis, dorso parce (1–4) atro-punctulatis, filamentis glabris, supra basin affixis; ovarium ad apicem minute rufo-tomentellum; stylus basi breviter pilosus.

A tree 4 to 6 m. high. Branchlets rather thick, at first minutely appressed rufous-lepidote. Leaves with petioles 1.5 to 2.5 cm. long, narrowly oblong or oblong-elliptic, 8.5 to 19 cm. long, 2.2 to 4.6 cm. wide, apex and base acuminate, margin somewhat repand, nearly entire, membranaceous, glabrous above, sparsely and minutely lepidote below, main lateral veins usually 18 on each side, nearly horizontal, prominulous on under-surface, picta numerous, mostly short-linear. Inflorescence axillary, many-flowered, paniculate, thyrsoid, 8 to 9 cm. long, sparsely lepidote or glabrous, pedicels up to 6.5 mm. long, much exceeding bracteoles; flowers before anthesis about 5 mm. long, finely rufous-puberulent; sepals united at base, narrowly triangular, about 0.9 mm. long, punctate; petals tomentose within, narrowly lanceolate-attenuate, 5 mm. long, united at base, linear-punctate; stamens 3 to 3.2 mm. long, anthers apiculate, 1.7 to 2 mm. long, dorsally few (1–4), black-punctate, filaments glabrous, subequaling anthers, attached slightly above base of petals; ovary rufous-tomentellous at apex, base of style short-pilose.—CHIRIQUÍ: valley of the upper Río Chiriquí Viejo, alt. 1300–1900 m., July 27, 1937, *Peggy & Gene White 27* (Herb. Univ. Michigan, TYPE).

Another collection, *Woodson, Allen & Seibert 798,* from vicinity of Casita Alta, Volcán de Chiriquí, Province of Chiri-

quí, Panama, June 28–July 2, 1938, at alt. of 1500–2000 m., is referable here, but differs in having smaller narrowly elliptic leaves. These collectors describe the fruits as "purple-black, depressed spherically, 1.2 cm." in diam. The flowers are reported to be pale pink or pink with sweet odor.

P. Seibertii is closely related to *P. melanosticta* (Schlechtd.) Hemsl., a species of Mexico and northern Central America, from which it may be differentiated by the entire or slightly repand, narrower, very thin, predominantly oblong leaves, and the paucity of pubescence throughout. The other related species, *P. macrophylla* Rusby of Bolivia, has much smaller anthers shorter than the filaments, as well as other marked differences.

VITACEAE

CISSUS EROSA L. C. Rich.—COCLÉ: thickets between Las Margaritas and El Valle, Aug. 8, 1938, *Woodson, Allen & Seibert 1763*. *C. erosa* is abundant in the Antilles, and has been collected several times in British Guiana, but this is apparently its first record in Central America. It was seen but once in the vicinity where the collection was made.

GUTTIFERAE

(P. C. Standley, Chicago)

HYPERICUM **Woodsonii** Standley, sp. nov. Herba perennis dense caespitosa omnino glabra, caulibus numerosis 3–8 cm. longis suberectis, saepe plus minusve intertextis angulatis dense foliatis; folia parva internodiis multo longiora sessilia oblonga vel oblanceolato-oblonga obtusa vel subacuta plerumque 3–8 mm. longa, basin versus paullo cuneato-angustata dense punctata, marginibus saepe plus minusve revolutis; flores terminales solitarii breviter pedunculati; sepala viridia 4–5 mm. longa tenuiter nervata anguste oblonga, apice apiculato-acutata; petala lutea sepalis aequilonga; styli 3 erecti 1 mm. longi et ultra; capsula ovoideo-oblonga 4 mm. longa apice in stylos sensim attenuata 1-locularis; semina numerosa oblonga ochracea 0.6 mm. longa.—CHIRIQUÍ: forming mats on potrero, Loma Larga to summit, Volcán de Chiriquí, alt. 2500–3380 m., July 4–6, 1938, *Woodson, Allen & Seibert 1040* (Herb. Field

Mus., TYPE; duplicate in Herb. Missouri Bot. Garden). Prostrate in potrero, Potrero Muleto, Volcán de Chiriquí, 3120 m., July 19, 1938, *Mrs. M. E. Davidson 1048* (Herb. Field Mus.).

From all other species of *Hypericum* known from southern Central America this is conspicuously different in its low, depressed habit, the plant being perennial and forming dense, interlaced mats.

MYRTACEAE

(P. C. Standley, Chicago)

EUGENIA **salamancana** Standley, sp. nov. Arbor 6-metralis, ramulis crassiusculis rigidis teretibus, novellis dense pilis brevibus rigidulis patentibus pilosis, internodiis brevibus; folia mediocria breviter petiolata subcoriacea, petiolo crasso 5–7 mm. longo dense breviter piloso; lamina oblonga vel ovali-oblonga 7–9 cm. longa 2.5–4 cm. lata, apice rotundata atque subito caudato-acuminata, acumine ca. 1 cm. longo angusto attenuato, basi anguste rotundata, supra subopaca, ad costam subimpressam minute pilosula, aliter glabra, nervis venisque obsoletis, subtus fere concolor, ad costam prope basin laminae pilosa, aliter glabra, costa gracili elevata, nervis lateralibus utroque latere ca. 12 sed obscuris, venis omnino occultis; flores ut videtur e ramis defoliatis nascentes solitarii(?) sessiles vel brevissime pedicellati, perfecti non visi.—CANAL ZONE: vicinity of Salamanca Hydrographic Station, Río Pequení, alt. 80 m., July 28–29, 1938, *Woodson, Allen & Seibert 1570* (Herb. Field Mus., TYPE; duplicate in Herb. Missouri Bot. Garden).

In leaf characters the species is unlike any other known from the region of the Isthmus, the nervation, except for the costa, being obscure or obsolete. The form of the inflorescence, although its structure is not well established, likewise appears to be quite distinctive.

MELASTOMACEAE

(H. A. Gleason, New York)

CENTRONIA PHLOMOIDES Triana—CHIRIQUÍ: vicinity of Casita Alta, Volcán de Chiriquí, alt. ca. 1500–2000 m., June 28–July 2, 1938, *Woodson, Allen & Seibert 842.* Previously known from Costa Rica.

Miconia lindenii Naud.—chiriquí: Finca Lérida to Boquete, alt. ca. 1300–1700 m., July 8–10, 1938, *Woodson, Allen & Seibert 1143.* Previously known from Costa Rica and Venezuela.

Blakea **Woodsoni** Gleason, sp. nov. (Sect. *Pyxidanthus).* Arbuscula 5–7 m. alta. Rami irregulariter 4-angulati, internodiis circa 10 mm. longis paulo incrassatis, superne furfuraceo-hispidi, pilis curvatis crasse subulatis fere 1 mm. longis. Petioli crassi, 12–25 mm. longi, sicut rami sparse hispidi. Laminae chartaceae obovato-oblongae, usque 11 cm. longae 7 cm. latae, apice subrotundatae ad apiculum triangularem brevem, integrae, basi late cuneatae, vix 3-pli-nerviae, supra glabrae arctissime brunneo-punctulatae, subtus hinc inde brevissime hispidulae, praecipue ad venas. Flores solitarii ex axillis superioribus, pedicello 6 cm. longo, hispidulo, glabrescenti. Bracteae per paria connatae, pari exteriori 12 mm. longo primo hispidulo mox glabrescenti, margine vix 2-lobato; bracteae interiores quam exteriores 3 mm. longiores, glabrae, margine integro. Calyx quam bracteae interiores 7 mm. longior, glaber, lobis 6, semicircularibus, paulo retusis et tuberculato-apiculatis. Petala anguste triangulari-obovata, alba, 4 cm. longa. Antherae semi-ovatae 7 mm. longae. Stylus gracilis, ad stigma punctiforme angustatus.—chiriquí: vicinity of Casita Alta, Volcán de Chiriquí, alt. 1500–2000 m., July 1, 1938, *Woodson, Allen & Seibert 951* (Britton Herb., New York Bot. Garden, type). It is at once distinguished from other Panama species by its totally connate bracts. The hairs of the stem, peduncles, and bracts are very easily detached.

LECYTHIDACEAE

Gustavia brachycarpa Pittier, Contr. U. S. Nat. Herb. **26**: 3. 1927.—chiriquí: swampy forests, west of Remedios, June 24, 1938, *Woodson, Allen & Seibert 787.* As far as we are aware, this is the first record of this peculiar specimen since the collection of the type by Pittier in 1911. The specimens of Pittier, from near San Felix, in the same general vicinity of our trees, were in fruit only. Ours are in full flower and young fruit. In bloom, the trees of *G. brachycarpa* are by far the most showy

of the low forests of the country-side. The petals are pure white, 6, broadly obovate-oblong, and somewhat unequal, 4.5–5.0 cm. long, 2.2–2.5 cm. broad, broadly rounded, essentially glabrous within, but very densely and minutely puberulent-papillate without. The stamens are exceedingly numerous, forming a regular, involuted cup 1.5 cm. deep; the anthers are connivent, oblongoid, 0.2 cm. long, and dehisce apically. The handsome flowers are borne singly or in pairs, and are slightly fragrant. Pittier's description of the leaves, fruits, and branches is accurate, and corresponds very closely to our specimens.

VACCINIACEAE

(W. H. Camp, New York)

COMAROSTAPHYLIS **chiriquensis** Camp, sp. nov. Frutex 1–3 m., ramis pubescentibus; folia rectangulo-ovata, petiolo 5–8 mm. longo, basi cuneata vel acuta, apice acuta, subcoriacea, 5–6 cm. longa, 1.0–1.5 cm. lata, supra glabra, subtus in foliis adultis dense ferrugineo- vel griseo-lanata, margine obscure undulata vel integerrima, revoluta; inflorescentia terminalis, paniculata, ubique obscure albido-puberula et plus minusve ferrugineo-pilosa, pilis glandulosis; pedicelli 2–3 mm. longi; bractea subacuminata; calyx 5-lobus, lobis ovato-acuminatis circ. 1.5 mm. longis, puberulis et sparse glandulosis; corolla globoso-urceolata, circ. 5 mm. longa, alba, extra obscure farinacea vel puberula, intra puberula, apice manifeste contracta, breviter 5-lobata, lobis puberulis; stamina 10, filamentis basin versus dilatatis, dense pubescentibus, circ. 2 mm. longis, antheris circ. 1.5 mm. longis, bicornutis; ovarium elongato-globosum, pubescens.—CHIRIQUÍ: Loma Larga to summit, Volcán de Chiriquí, alt. ca. 2500–3380 m., July 4–6, 1938, *Woodson, Allen & Seibert 1033* (Britton Herb., New York Bot. Garden, TYPE).

This species, although closely related to *C. arbutoides* Lindl., may be distinguished from it by the greater number of conspicuous gland-hairs on the rachis and pedicels, these often being 1 mm. long, and the absence of the rusty-brown, woolly tomentum on these same structures—a characteristic feature

of *C. arbutoides.* In this last, all the inflorescence and often the floral structures are so covered with this tomentum that their surfaces are invisible, whereas in *C. chiriquensis* this is not the case. An additional interesting feature of this new species is the presence on the lower surface of the leaf of scattered gland-hairs on and near the midvein as well as on the petioles. Minute fruiting bodies of some fungus, similar in appearance to these glands, but easily recognizable as such, are also present on various organs of the type.

GENTIANACEAE

(F. P. Jonker, Utrecht; Halenia by C. K. Allen, Jamaica Plain, Mass.)

LISIANTHUS CHELONOIDES L.f.—CHIRIQUÍ: Finca Lerida to Boquete, alt. ca. 1300–1700 m., July 8–10, 1938, *Woodson, Allen & Seibert 1111.* Previously recorded from Peru, Brazil, the Guianas, and the West Indies.

SCHULTESIA BRACHYPTERA Cham. forma HETEROPHYLLA (Miq.) Jonk.—PANAMÁ: boggy grasslands and marginal thickets, between Pacora and Chepo, alt. ca. 25 m., Aug. 1, 1938, *Woodson, Allen & Seibert 1647.* Previously known from Brazil, Venezuela, the Guianas, and Mexico.

HALENIA **Woodsoniana** C. K. Allen, spec. nov. Herba perennis (?), caule basi ramoso procumbente; ramulis floriferis pluribus erectis usque ad 7 dm. altis; ramulis sterilibus foliosis quam ramulis floriferis circiter ½ brevioribus (± 3 dm. altis); internodiis inferioribus brevibus (1.5–3 cm.) superioribus longioribus (4–6.5 cm.); foliis sessilibus lineari-lanceolatis acuminatis leviter 3-nerviis, nervo medio prominente, usque ad 6 cm. longis et 0.7 cm. latis; inflorescentia terminalis axillarisve cymosa laxa pauciflora; calyce usque ad 1 cm. longo et ad ca. ¾ corollae longitudinem aequante; lobis 3-nerviis lanceolatis acuminatis; corollae lobis ovalibus acutis leviter erosis; calcaribus usque ad ⅓ corollae longitudinem aequantibus horizontalibus ad leviter ascendentibus; staminibus 0.5 cm. longis; capsula late lanceolata usque ad 1.7 cm. longo.—CHIRIQUÍ: Volcán de Chiriquí, ca. 2500–3380 m., Loma Larga to summit, July 4–6, 1938, *Woodson, Allen & Seibert 1052* (Herb. Missouri Bot. Garden, TYPE).

The above species is distinctive because of the much-branched stem, somewhat procumbent at the base, the short leafy sterile shoots arising from the main stem, and the tall spreading, loosely flowered inflorescence, the pedicels of which are often pendulous. The species, the sole representative of the genus in Panama thus far found, is most closely related to *Halenia rhyacophila* Allen from Costa Rica.

APOCYNACEAE

Rauwolfia hirsuta Jacq. var. **glabra** (Muell.-Arg.) Woods. comb. nov. (*R. canescens* L. var. δ *glabra* Muell.-Arg. Linnaea **30**: 394. 1860).—panamá: Isla Taboga, thickets near sea-level, July 23–24, 1938, *Woodson, Allen & Seibert 1530.*

Forsteronia spicata (Jacq.) G. F. W. Meyer—panamá: Isla Taboga, abundant, in thickets along rocky shore, July 23–24, 1938, *Woodson, Allen & Seibert 1551.* This species is of interest since it is predominantly a Caribbean element found at intervals upon the continent from southern Mexico to northern Colombia, and in Cuba. Upon the Pacific coast it has been reported only from Salvador and Costa Rica. This is the first record of the species from Panama.

Stemmadenia obovata (H. & A.) K.Sch. var. mollis (Benth.) Woods.—los santos: between Los Santos and Guararé, July 11, 1938, *Woodson, Allen & Seibert 1200;* vicinity of Las Tablas, alt. 15 m., Sept. 12, 1938, *Allen 812.* Previously recorded from southern Mexico to Costa Rica, where it is relatively limited in distribution; also very local in western Ecuador.

Prestonia **remediorum** Woodson, spec. nov. Frutex volubilis, ramis ramulisque crassiusculis ferrugineo-hirtis. Folia obovato-elliptica apice breviter acuminata basi obtuse cuneata 15–18 cm. longa 9–11 cm. lata membranacea opaca supra subtusque ferrugineo-pilosula, petiolis 1.5 cm. longis, appendicibus stipulaceis intrapetiolaribus pectinatis ca. 0.25 cm. longis. Inflorescentia lateralis simplex pluriflora corymbiformis folia ca. ½ aequans, pedicellis ca. 1 cm. longis ferrugineo-hirtellis, bracteis foliaceis oblongo-lanceolatis acuminatis 1.0–1.5 cm. longis foliaceis ferrugineo-puberulis. Calycis

lobi oblongo-lanceolati acuminati 1.7–1.8 cm. longi foliacei dense ferrugineo-hirtelli, squamellis profunde pectinatis subcallosis ca. 0.2 cm. longis appendicibus stipulaceis similibus. Corollae luteae extus dense ferrugineo-velutinae tubus subinfundibuliformis in alabastrum submaturum 2 cm. longus basi ca. 0.15 cm. diam., faucibus ca. 0.35 cm. diam.; lobi obovato-dolabriformes acuminati 1.7 cm. longi. Anthera 0.7 cm. longa glabra apice paululo exserta. Stigma fusiforme 0.3 cm. longum; ovarium ovoideum ca. 0.15 cm. altum glabrum; nectaria 5 carnosa basi concrescentia ovarium aequantia. Folliculi ignoti.—CHIRIQUÍ: thicket, between Río Chiriquí and Remedios, alt. ca. 15–50 m., July 11, 1938, *Woodson, Allen & Seibert 1180* (Herb. Missouri Bot. Garden, TYPE).

When this species was collected, it was mistaken for *P. isthmica* Woods., an endemic of Costa Rica. The leaves of *P. remediorum* are quite distinct, however, by reason of their cuneate base, and the conspicuous, pectinate calycine squamellae are quite unlike those of any species with which I am familiar.

FERNALDIA **speciosissima** Woodson, spec. nov. Frutex volubilis alte scandens, nec foliis nec calycibus necque ovariis visis; corollae speciosissimae albidae extus omnino glaberrimae tubo proprio 2.5–2.8 cm. longo basi ca. 0.25 cm. diam. stricto haud gibboso, faucibus tubulosis 2.6–2.8 cm. longis intus dense arachnoideo-villosis, ostio ca. 0.6 cm. diam., lobis oblique obovatis obtusis 2.8–3.0 cm. longis patulis utrinque glaberrimis; antheris anguste lanceolato-sagittatis basi obtuse auriculatis 1 cm. longis glaberrimis; stigmate fusiformi basi minute digitato-appendiculato 0.3 cm. longo.—CHIRIQUÍ: thickets, between Río Chiriquí and Remedios, alt. 15–50 m., July 11, 1938, *Woodson, Allen & Seibert 1179* (Herb. Missouri Bot. Garden, TYPE).

It is exasperating to have to describe this species merely from several detached corollas found at the base of a tall tree supporting the liana. Efforts to obtain more ample material being futile at the time of collection, complete confidence none the less may be placed in the generic identification of the corollas (which, of course, contain the stamens and stigma as

is customary in the Echitoideae). The anthers, stigma, and arachnoid internal villosity of the corolla are all unmistakable characters, although the villosity differs from that of the three other known species of the genus in being limited to the throat. The corollas of *F. speciosissima* much surpass those of the other known species, and the narrowly tubular throat is quite distinct. Eastern Chiriquí is one of the least known and most promising floristic regions of Panama, as is graphically illustrated by the discovery of both *Prestonia remediorum* and *Fernaldia speciosissima,* literally within a stone's throw of one another.

ASCLEPIADACEAE

Macroscepis **panamensis** Woodson, spec. nov. (fig. 1). Suffrutex volubilis; ramis dense luteo-pilosis pilis dissimilibus tum brevibus simplicibus tum multo longioribus multicellularibus sicut ad petiolos et pedunculos pedicillosque; foliis oppositis petiolatis latissime ellipticis vel obovato-ellipticis apice attenuate subcaudato-acuminatis basi late auriculatis 14–17 cm. longis 9–11 cm. latis membranaceis opacis supra sparse strigosis subtus farinulento-puberulis nervo medio subtus luteo-pilosis, petiolo 2 cm. longo; inflorescentiis axillaribus alternatis umbelliformibus 6–8-floris, pedunculo ca. 2 cm. longo; bracteis lineari-lanceolatis foliaceis ca. 1 cm. longis vel infra dense luteo-pilosis; pedicellis 0.8 cm. longis similiter vestitis; calycis laciniis late ellipticis acuminatis foliaceis 0.5–0.6 cm. longis minute puberulis margine ciliatis intus eglandulosis; corollae salverformis extus omnino glaberrimae pallide luteo-viridis tubo campanulato 0.9–1.0 cm. longo medio inflato ibique ca. 0.8 cm. diam. faucibus constrictis minute hispidulis ceterumque glaberrimis, limbo patulo 1.8–1.9 cm. lato intus minute hispidulo-papillato ca. dimidio lobato lobis obtusis, coronae squamis tubo fere ad fauces adnatis apice subquadratis integris introrsum replicatis basi calloso-geniculatis tubo stamineo adnatis; gynostegio subsessili ca. 0.45 cm. alto, antheris brevissime appendiculatis basi coronae adnatis, stigmate obscure 5-lobato ca. 0.3 cm. diam.; polliniis oblique pyriformibus valde compressis ca. 0.1 cm. longis, caudiculis multo

brevioribus, retinaculo oblongo caudiculum aequante; folliculis ignotis.—PANAMÁ: thickets near Capira, July 12, 1938, *Woodson, Allen & Seibert 1228* (Herb. Missouri Bot. Garden, TYPE); liana in thickets, Isla Taboga, July 23–24, 1938, *Woodson, Allen & Seibert 1432.*

Macroscepis panamensis differs from *M. tristis* (Seem.) Benth., the only species of the genus previously known from Panama, and apparently collected but once (*Seemann 158,*

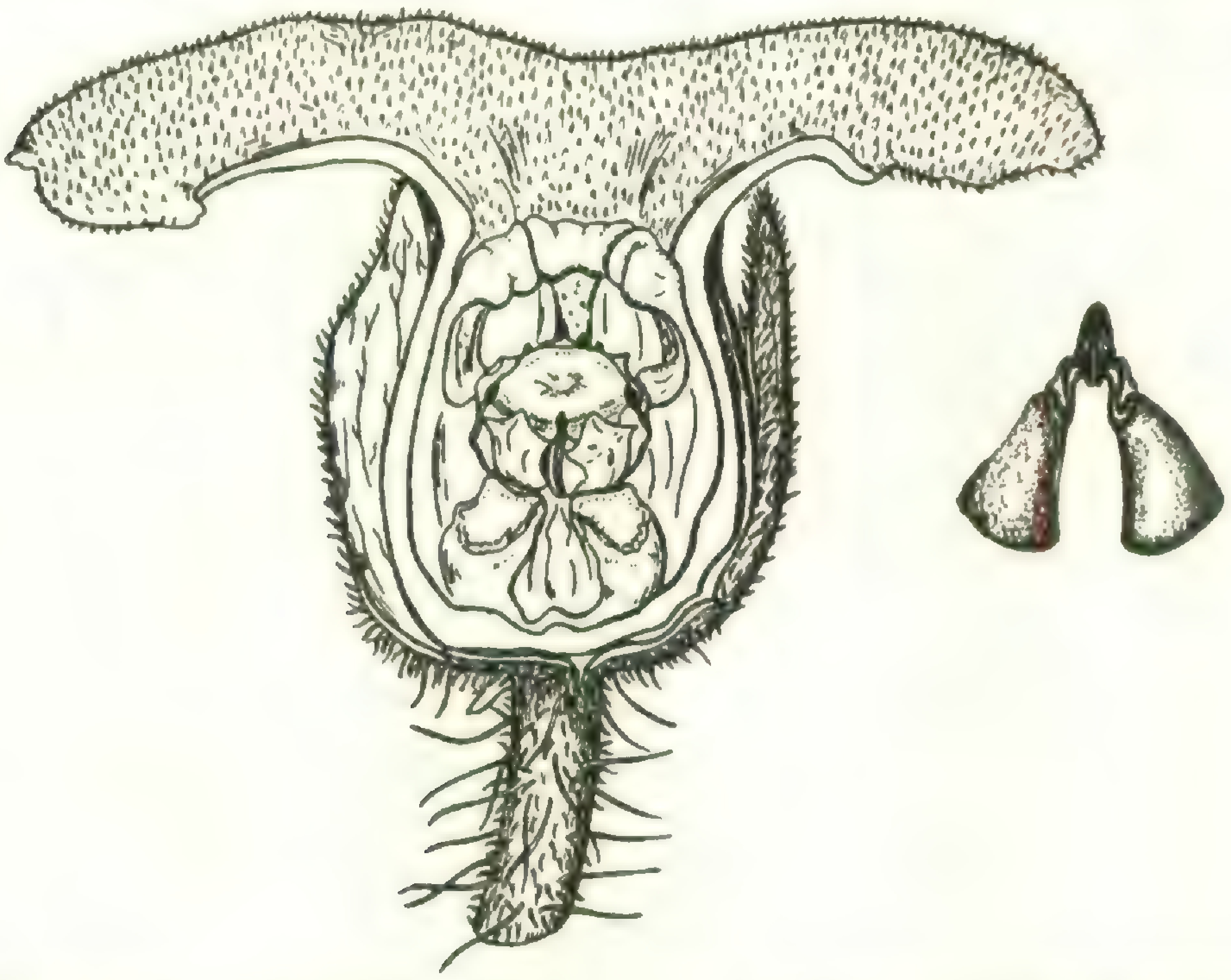


Fig. 1. *Macroscepis panamensis* Woodson. Flower in section, and pollinia. (Drawing by A. A. Heinze.)

in the Province of Veraguas near Natá), principally in the flowers. The corolla of *M. tristis* is described as absolutely glabrous, the tube light brown, and the limb dark chocolate. It is surprising that *Macroscepis* has not been collected previously in the province of Panama, as it is apparently widespread.

MARSDENIA CRASSIPES Hemsl.—PANAMÁ: thickets near Arraiján, alt. ca. 15 m., June 22, 1938, *Woodson, Allen & Seibert 779.* This is apparently the first collection of this endemic species since the discovery of the type specimen by Dr. Sutton Hayes. The corolla is greenish-yellow, and the corona seg-

ments, far surpassing the anther membranes, overhang the rostrate stigma.

MARSDENIA MACROPHYLLA (H. & B.) Fourn.—LOS SANTOS: thickets between Los Santos and Guararé, July 11, 1938, *Woodson, Allen & Seibert 1197.* As far as I am aware, this is the second time this species has been collected in Panama. I have been unable to examine the first, collected by Seemann (n. *611)* near the city of Panamá, but specimens in the herbarium of the Missouri Botanical Garden, cited as of this species by Rothe (Engl. Bot. Jahrb. **52**: 416. 1915) from Central America, have obtuse or rounded leaf bases and anther membranes slightly surpassing the crown segments (used as a key character by Rothe). On the other hand, our specimen has obviously cordate leaves, and the crown segments equal, or even slightly surpass the anther membranes.

GONOLOBUS EDULIS Hemsl.—BOCAS DEL TORO: thickets near Guabito, Aug., 1938, *J. H. Permar s.n.* Previous records of this plant have indicated its range from southern Mexico to Costa Rica. The material thoughtfully sent by Mr. Permar consists of follicles 7–8 cm. long, approximately 5 cm. in diameter, which bear conspicuous wings about 1 cm. broad.

GONOLOBUS **Monnicheanus** Woodson, spec. nov. (fig. 2). Frutex volubilis. Ramuli graciliusculi ferrugineo-pilosuli inferne glabrati. Folia opposita longiuscule petiolata, ovato-oblonga apice abrupte subcaudato-acuminata basi latiuscule cordata 4.9–9.0 cm. longa 2.5–4.5 cm. lata membranacea concoloria supra sparse ferrugine hispidulo-pilosula nervo medio basi pauciglanduligera subtus sparsiuscule ferrugineo-strigosula; petiolus 2.5–3.0 cm. longus pilosulus. Inflorescentia lateralis alternata longiuscule pedunculata umbelliformis flores mediocres dilute virido-luteos 10–30 gerens; pedunculi 3–5 cm. longi minute pilosuli; bracteae lineari-lanceolatae vix 0.2 cm. longae; pedicelli 2.5–3.5 cm. longi gracili minute pilosuli; calycis laciniae ovato-lanceolatae anguste acuminatae 0.8 cm. longae apicibus valde reflexis glabris caeterumque ferrugineo-pilosulae, squamellis alternatis solitariis dentiformibus ca. 0.15 cm. longis; corolla rotata dilute viridi-lutea extus dense

puberulo-papillata, tubo late conico ca. 0.5 cm. profundo basi ca. 0.1 cm. diam. intus dense minuteque hispidulo, lobis late ovatis obtuse acuminatis 1 cm. longis basi ca. 0.7 cm. latis apice valde reflexis; gynostegium anguste (ca. 0.2 cm.) stipitatum subalato-costatum, stigmate 5-gono ca. 0.5 cm. diam., antheris brevissime rotundeque apiculatis, polliniis compresse ovoideis ca. 0.1 cm. longis caudiculas subaequantibus, corpusculo compresse oblongo-sagittato ca. 0.025 cm. longo; corona exterior latissime campanulata 5-partita carnosa saturate lutea

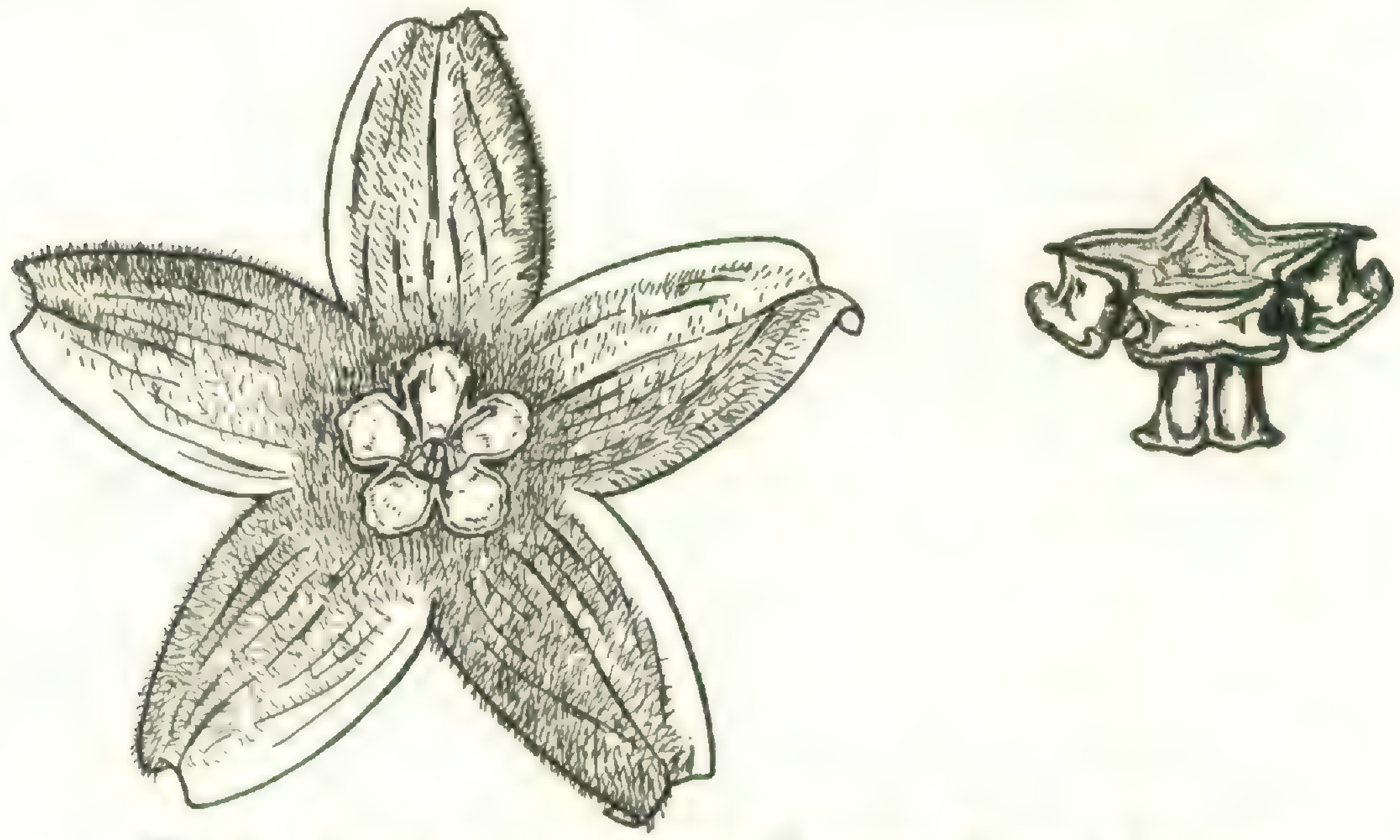


Fig. 2. *Gonolobus Monnicheanus* Woodson. Flower with gynostegium removed to show corona; gynostegium. (Drawing by A. A. Heinze.)

glabra corolla basi adnata ca. 0.7 cm. diam. ca. 0.2 cm. profunda, corona interior antheris adnata, squamis subreniformibus ca. 0.25 cm. latis 0.15 cm. longis patulis; folliculis ignotis.—Chiriquí: thickets, between Finca Lérida and Boquete, alt. 1300–1700 m., July 8–10, 1938, *Woodson, Allen & Seibert 1108* (Herb. Missouri Bot. Garden, type).

This species is named in honor of Mr. Tollef B. Mönniche, the master of Finca Lérida and a discriminating and enthusiastic naturalist, in grateful memory of his innumerable kindnesses, not only to itinerant botanists, but to the multitude of other pilgrims who make their way, sure of an understanding

welcome, to his remarkable establishment on the high slopes of the Volcán de Chiriquí. *G. Monnicheanus* is evidently closely related to both *G. edulis* Hemsl. and *G. dubius* Pittier, but differs conspicuously from the former by the remarkable development of the outer corona, and from the latter in the hispidulous indument of the corolla.

CUSCUTACEAE

(T. G. Yuncker, Greencastle, Ind.)

Cuscuta **Woodsonii** Yuncker n. sp. (fig. 3). Caules crassi. Flores 4 mm. longi ab floris base ad corollae sinum, subsessiles in dispersis inflorescentibus compactis. Calycis lobi orbiculari-ovati, late imbricati, obtusi, plus minusve carinati. Corolla campanulata, lobi late ovati, obtusi, auriculati. Stamina lobis corollae dimidio breviora, antherae ovoideae, filamenta subulata, non teretia. Scalae exsertae, oblongae, fimbriatae. Styli ovarium ovoideum circa aequantes, paulo subulati. Capsula depresso-globosa, usque ad 6 mm. diametro, circumscissilia, apertura intrastylaris lata. Semina 4, circ. 2.5 mm. longa, ovalia, hilo oblongo, diagonali.

Stems coarse. Flowers membranous or somewhat fleshy, about 4 mm. in length from the base to the corolla sinuses, or 7 cm. to the apex of the corolla-lobes when erect, subsessile in scattered, few-flowered, compact clusters. Calyx rather loose about the corolla and scarcely reaching the sinuses, lobes orbicular-ovate, broadly overlapping, obtuse, fleshy in the median and basal parts, becoming thin towards the slightly uneven edges, commonly one or more lobes carinate. Corolla campanulate, lobes about as long as the tube, or slightly shorter, broadly ovate, obtuse, strongly auriculate at the base and broadly overlapping, upright to spreading. Stamens reaching to about the middle of the corolla-lobes, filaments very subulate, flattened (not terete), somewhat longer than the ovoid anthers. Scales prominent, reaching the anthers, oblong, fringed with medium-length processes about the top and sparingly so along the sides, bridged below the middle, somewhat thick and fleshy toward the attached basal part. Styles about equal to the ovoid ovary, stout and somewhat subulate.

Capsule depressed-globose, up to 6 mm. in diameter, intrastylar aperture large, becoming definitely circumscissile when mature although this character may be rather obscure in young fruit, surrounded by the withered corolla which eventually splits as the capsule enlarges. Seeds 4, about 2.5 mm. long, oval in outline, hilum oblong, oblique.—Chiriquí: vicinity of Casita Alta, Volcán de Chiriquí, alt. 1500–2000 m., June

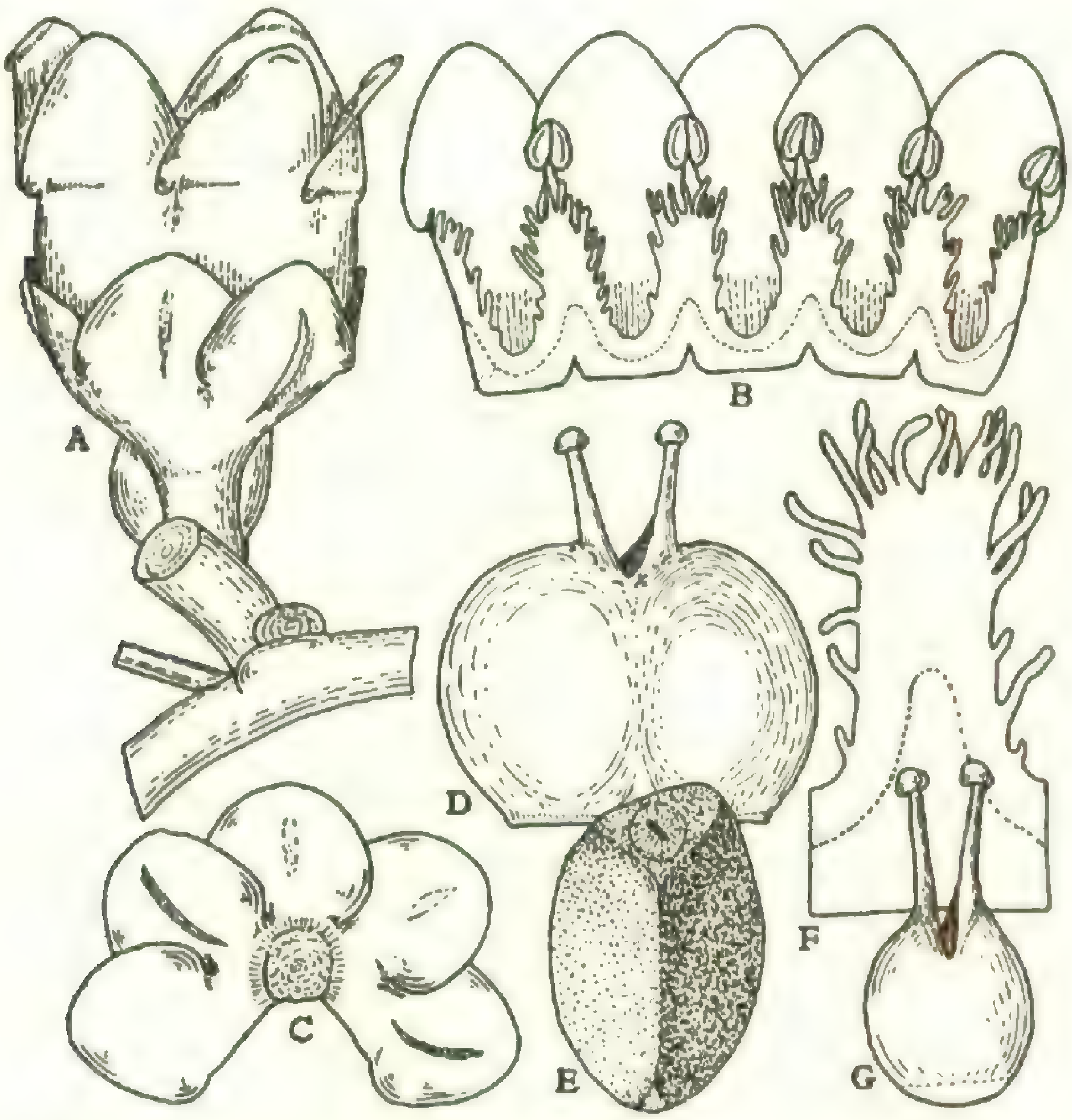


Fig. 3. *Cuscuta Woodsonii* Yuncker n. sp.: *A*, flower × 5; *B*, opened corolla × 5; *C*, opened calyx × 5; *D*, capsule × 5; *E*, seed × 10; *F*, individual scale × 10; *G*, ovary × 5.

28–July 2, 1938, on a species of *Eupatorium* (?), *Woodson, Allen & Seibert 950* (Herb. Missouri Bot. Garden, TYPE).

The genus *Cuscuta* appears to be poorly represented in Panama. The only species previously known to occur there is *C. trichostyla* Engelm. which is represented, so far as I know, by only a single specimen collected by Tweedie. *C. Woodsonii* differs from *C. trichostyla* in most of the distinctive characters given below. It appears to be most closely allied with those

included in the subsection Subulatae of the section Eugrammica although the styles do not become so strongly subulate as do those of the species included there. Its chief distinguishing features are the size of the flowers, fruit, and seeds, which are among the largest in the genus; the strongly subulate and flattened filaments; the prominent, oblong scales; and especially the prominently auriculate corolla-lobes, a character more strongly developed here than in any other known species.

BIGNONIACEAE

Arrabidaea obliqua (HBK.) Bur.—panamá: Gorgona Beach, vic. Gorgona, fr. Aug. 7, 1938, *Woodson, Allen & Seibert 1688.* Previously known from Venezuela and Colombia.

Arrabidaea Pleei DC.—coclé: between Aguadulce and Antón, alt. 15–50 m., July 12, 1938, *Woodson, Allen & Seibert 1224.* panamá: beach at Nueva Gorgona, Aug. 7, 1938, *Woodson, Allen & Seibert 1689.* Previously known from Venezuela and northern Colombia.

Lundia corymbifera (Vahl) Sandw.—chiriquí: banks of the Río Chiriquí, vic. Chiriquí, alt. 15 m., July 11, 1938, *Woodson, Allen & Seibert 1178.* Although the species has been reported from Costa Rica, and occurs frequently from Colombia to Brazil, its existence in Panama has previously been unknown.

Saldanhaea Seemanniana O. Ktze.—canal zone: Victoria Fill, near Miraflores Locks, fl. April 2, 1939, *P. H. Allen 1755.* panamá: Río de Panamá, near Capira, fl. April 4, 1938, *P. H. Allen 730;* vic. Capira, fr. July 15, 1938, *Woodson, Allen & Seibert 1310.* coclé: vic. of Penonomé, alt. 15–300 m., fl. Feb. 23–March 22, 1908, *R. S. Williams 522* (U. S. Nat. Herb. type of *Adenocalymma cocleensis* Pittier). Although previously reported from Panama by O. Kuntze, more recently the plant has been described as *Adenocalymma cocleensis,* a synonymous name.

Tabebuia heterotricha (DC.) Hemsl.—canal zone: Ancon, fl. May 1, 1934, *J. P. Keenan 323* (U. S. Nat. Herb.); vic. Summit, fl. March 17, 1934, *B. Avilla 314* (U. S. Nat. Herb.). panamá: Alhajuela, Chagres Valley, alt. 30–100 m., st. May 12–15,

1911, *H. Pittier 3501* (Gray Herb.); vic. of Chorrera, fl. March 5, 1939, *P. H. Allen 1698;* Sabanas, fl. April 1933, *Bro. Paul 307* (U. S. Nat. Herb.). Frequently confused with *Tabebuia chrysantha* (Jacq.) Nichols., but distinguishable by having a very densely woolly calyx, covered with long simple hairs and a much shorter stellate tomentum which can be seen only by the removal of the longer hairs.

The following additional specimens extend the range from Venezuela and Panama to Costa Rica and Nicaragua: COSTA RICA: without definite locality, fl. April 12, 1923, *A. M. Brenes 3876* (Herb. Field Mus.). NICARAGUA: south of Managua, fl. March 3, 1922, *J. M. Greenman & M. T. Greenman 5714* (Herb. Missouri Bot. Garden).

TABEBUIA PALMERI Rose.—PANAMÁ: vic. Bejuco, fl. Feb. 9, 1939, *P. H. Allen 1630*. Previously known to extend from the state of Michoacan in Mexico to Nicaragua.

The species flowers without leaves, making accurate determination impossible at the present time. However, flowers, pubescence and branchlets agree well with typical material of the species.

GESNERIACEAE

(C. V. Morton, Washington)

TUSSACIA **Woodsoni** Morton, sp. nov. Herba terrestris, caulibus non ramosis, apicem versus dense pilosulis; folia opposita aequalia, subsessilia, petiolo vix 5 mm. longo; lamina foliorum ovalis, usque ad 15 cm. longa et 7 cm. lata, acuta, basi longe (3–4 cm.) decurrens, tenuiter membranacea, valde crenata, supra scaberula, subtus praecipue in venis pilosula, venis primariis ca. 7-jugis; inflorescentia umbellata, ca. 4-flora, pedunculo communi axillari solitario, 2.3–2.8 cm. longo, pilosulo, apice bibracteato, bracteis linearibus, ca. 7 mm. longis, integris, pilosulis, pedicellis 12–13 mm. longis, pilosulis, apice vix incrassatis; calyx aurantiacus, ca. 15 mm. longus, campanulatus, externe scaberulo-strigillosus, tubo ca. 12 mm. longo, 10 mm. lato, lobis late triangularibus, ca. 3 mm. longis, acutis, glanduloso-denticulatis, dentibus 1 vel 2 utroque latere; corolla flava et aurantiaca, ca. 18 mm. longa, tubulosa, externe pilosa, limbo

patente, ca. 15 mm. lato.—CHIRIQUÍ: between Río Chiriquí and Remedios, alt. 15–50 m., July 11, 1938, *Woodson, Allen & Seibert 1195* (U. S. National Herb., no. 1,748,081, TYPE).

I had at first identified this collection as *Tussacia Friedrichsthaliana* Hanst., but Dr. Woodson, who had collected the latter species twice (nos. *1614* and *1642*), told me that in the field he had considered it a distinct species, chiefly on the basis of the differently colored calyx (deep orange rather than pale yellow). With this in view I re-examined the material and have concluded that no. *1195* does in fact represent an undescribed species. All the collections of *T. Friedrichsthaliana* have the corolla glabrous, whereas no. *1195* has a distinctly pilose corolla. The different coloration of the calyx is not apparent in dried material, and requires field investigation to determine its importance. Both calyx and corolla evidently vary somewhat in color, at least according to collectors' field notes. *Woodson, Allen & Seibert* 1642 says, "calyx yellowish-green, corolla green with orange scarlet lines at base of lobes"; no. 1614 says, "corolla orange"; *Kenoyer* 536, "flowers yellow"; *Standley* 40952 and 41121, "calyx green, corolla orange"; *Seibert* 556, "flowers orange"; and *Seibert* 569, "flowers orange, streaked in corolla with reddish orange."

KOHLERIA **serrulata** Morton, sp. nov. *Moussonia.* Frutex ramosus, caulibus dense hirto-tomentosis, serius glabrescentibus, ca. 2 mm. diam., subteretibus; petioli usque ad 12 mm. longi, flavo-tomentosi; lamina foliorum ovato-lanceolata, usque ad 7.5 cm. longa et 4 cm. lata, acuminata, basi rotundata, chartacea, serrulata, supra scabro-pilosula, subtus dense pilosula, venis primariis ca. 7-jugis; flores solitarii, axillares, pauci, non pseudospicati, pedicello 15–18 mm. longo, 5 mm. supra basim bibracteato, bracteis subulatis, ca. 4 mm. longis, dense tomentosis; calycis pars adnata campanulata, ca. 2.5 mm. longa et 3 mm. lata, dense pilosa, pars libera 7 mm. longa, tubo brevissimo vix 1 mm. longo externe piloso intus glabro, lobis erectis lanceolatis 6 mm. longis et 2.2 mm. basi latis, acuminatis, apice non recurvatis, integris, margine non incrassatis, externe dense pilosis, intus sparse pilosulis; corolla aurantiaco-

rubra, 25 mm. longa, tubulosa, tubo basi non calcarato, in calyce erecto, basi 5.5 mm. lato, superne gradatim ampliato, vix ventricoso, in fauce non contracto, 9–11 mm. lato, externe dense pilosulo, intus glaberrimo, limbo brevi, lobis erectis, suborbicularibus, ca. 3 mm. longis, erosis, immaculatis; filamenta in basi corollae tubi inserta, cum tubo non adnata, inter se omnino libera, basin versus pilosa, superne glabra, non contorta, 22–25 mm. longa; antherae liberae, ca. 2 mm. longae, 1.5 mm. latae, loculis oblongis, non confluentes; ovarium (pars libera) conicum, brevissimum, dense pilosum; stylus rectus, glaber; stigma stomatomorphum; discus annularis, brevissimus, glaber, paullo undulatus.—CHIRIQUÍ: Bajo Mono, mouth of Quebrada Chiquero, along Río Caldera, alt. 1500–2000 m., July 3, 1938, *Woodson, Allen & Seibert 1609* (U. S. National Herb., no. 1,746,849, TYPE).

Perhaps related to *Kohleria elegans* (Dcne.) Loes. but distinguished by the solitary rather than umbellate flowers, the less sharply acuminate calyx-lobes, the included free anthers and glabrous style.

CAMPANEA **chiriquana** Morton, sp. nov. *Eucampanea.* Planta epiphytica, caulibus dense piloso-tomentosis, pilis brunneis multiseptatis; folia opposita paullo inaequalia, longe petiolata, petiolo usque ad 4 cm. longo, dense brunneo-tomentoso; lamina foliorum ovato-oblonga, usque ad 17 cm. longa et 9 cm. lata, apice cuspidato-acuminata, basi cuneata in petiolum decurrens, membranacea, dentata basi excepta, supra pilosula, subtus praecipue in venis dense brunneo-tomentosa, venis primariis 7- vel 8-jugis; inflorescentia umbellata triflora, pedunculo communi pendulo, valde elongato, ca. 20 cm. longo, dense brunneo-tomentoso, apice bibracteato, bracteis linearibus, ca. 9 mm. longis, dense tomentosis, pedicellis usque ad 5.5 cm. longis, dense tomentosis; calycis lobi lanceolati, 8–9 mm. longi, acuminati, non evidenter venosi, dense tomentosi; corolla pallide flava, maculata, ca. 2.5 cm. longa, tubo basi erecto, valde ventricoso, medio 1.8 cm. lato, faucem versus contracto, externe brunneo-piloso, limbo parvo, lobis rotundatis, intus glabris.—CHIRIQUÍ: vicinity of Casita Alta, Volcán de Chiri-

quí, alt. 1500–2000 m., June 28–July 2, 1938, *Woodson, Allen & Seibert 935* (U. S. National Herb., no. 1,747,001, TYPE).

Near *Campanea Oerstedii* (Klotzsch) Oersted, of Costa Rica, but with the pubescence of the stems and under-surface of the leaves more nearly tomentose (as in *C. Humboldtii*), the calyx-lobes smaller and not evidently nerved, and the corolla more prominently ventricose. The species of this genus are badly in need of a careful revision.

SOLENOPHORA **australis** Morton, sp. nov. Frutex 5 m. altus, caulibus atropurpureis obtusangulatis subquadrangulatis, glaberrimis; petiolus usque ad 4.5 cm. longus, fere glaber, apicem versus pilis sparsis flaccidis brunneis multiseptatis praeditus; lamina foliorum ovalis, usque ad 15 cm. longa et 8.5 cm. lata, acuminata, basi perspicue obliqua, rotundata, papyracea, valde biserrata, supra sparse pilosula, subtus in venis sparse scabro-pilosula, venis primariis ca. 9-jugis; flores subumbellati, pedunculo communi solitario, usque ad 4.5 cm. longo, 1.5 mm. diam., compresso, glaberrimo, ca. 3-floro, apice bibracteato, bracteis subulatis crassis ca. 1 cm. longis apice pilosulis, pedicellis ca. 1.7 cm. longis crassis glaberrimis medio bibracteolatis apice paullo incrassatis; calyx venosus, 3 cm. longus, externe fere glaber, pilis paucis minutis flaccidis multiseptatis apicem versus praeditus, intus dense pilosus, tubo subcylindrico, ca. 2.2 cm. longo, 1 cm. lato, basi late cuneato, lobis erectis ca. 8 mm. longis, triangularibus acuminatis margine glanduloso-denticulatis, dentibus 3 vel 4 utroque latere; corolla externe aurantiaca, intus flava, 8.5 cm. longa, externe parce pilosa, intus glabra, tubo 6.5 cm. longo, basi cylindrico, superne gradatim ampliato, vix ventricoso, apice 2.5 cm. lato, in fauce non contracto, limbo patente subbilabiato, lobis late obovatis vel suborbicularibus, utrinque glabris, apice subtruncatis erosis, intus marginem versus purpureo-maculatis; stamina basi corollae tubi inserta, filamentis latis glabris basi ca. 1.5 cm. connatis, antheris apice connatis, 4.5 mm. longis, 4 mm. latis, connectivo hastato glabro, loculis hippocrepiformibus, apice confluentibus, longitudinaliter dehiscentibus; stylus elongatus, compressus, ca. 2 mm. latus, valde pilosulus; stigma

latum stomatomorphum; ovarium inferum glaberrimum, placentae lamellae utrinque ovuliferae; disci glandulae 2 posticae, magnae, basi connatae, apice rotundatae, ca. 2.5 mm. longae, ubique dense pilosae.—CHIRIQUÍ: vicinity of Casita Alta, Volcán de Chiriquí, alt. 1500–2000 m., June 28–July 2, 1938, *Woodson, Allen & Seibert 847* (U. S. National Herb., no. 1,746,987, TYPE).

Closely related to *Solenophora calycosa* Donn. Smith, of Costa Rica, but distinguished by the entirely glabrous ovary, nearly glabrous calyx-tube, and glabrous stems and peduncles.

COLUMNEA TOMENTULOSA Morton—BOCAS DEL TORO: Río Cricamola, between Finca St. Louis and Konkintoë, alt. 10–50 m., Aug. 12, 1938, *Woodson, Allen & Seibert 1876.* Previously known from Nicaragua and Costa Rica.

COLUMNEA **panamensis** Morton, sp. nov. *Eucolumnea.* Frutex epiphyticus parce ramosus, caule subtereti parce strigoso ca. 8 mm. diam., ramulis brevibus, dense antrorse strigosis; folia opposita aequalia, breviter petiolata, petiolo ca. 4 mm. longo, strigoso-hirtello; lamina foliorum elliptica vel anguste elliptica, 4–4.5 cm. longa et 1.5–1.9 cm. lata, vix acuta, basi cuneata, chartacea, integra, utrinque dense strigoso-pilosa, immaculata, venis primariis 4-jugis; flores adscendentes solitarii axillares, pedicello 1.5 cm. longo, dense albido-tomentoso; calycis lobi liberi, lineari-oblongi, ca. 1.5 cm. longi, 4 mm. lati, acuti, basi angustati, integri, utrinque pilosi; corolla coccinea, 6.5–7 cm. longa, in calyce suberecta, basi postice gibbosa, tubo ca. 3 cm. longo, basi ca. 4 mm. lato, sursum ampliato sed non ventricoso, in fauce 10–11 mm. lato, non contracto, externe piloso, limbo valde bilabiato, galea erecta integra, 3–3.5 cm. longa, apicem versus ca. 1.4 cm. lata, lobis lateralibus cum galea alte connatis (1.8–2 cm.), partibus liberis deltoideis acutis, inferiore patente, lineari-oblongo, 1.5–1.7 cm. longo; filamenta pilosula, apice recurvata; antherae quadratim connatae, mox liberae, 2.6 mm. longae, 2.4 mm. latae, glabrae, loculis oblongis; ovarium dense albo-villosum; stylus elongatus pilosulus; stigma stomatomorphum; disci glandula crassa emarginata, ca. 2.3 mm. longa et 2.2 mm. lata, glabra.—CHIRIQUÍ:

vicinity of Casita Alta, Volcán de Chiriquí, alt. 1500–2000 m., June 28–July 2, 1938, *Woodson, Allen & Seibert 860* (Herb. Missouri Bot. Garden, TYPE).

Perhaps allied to *C. microcalyx* Hanst., of Costa Rica, but distinguished by the larger, longer-petiolate leaves, the different pubescence of the leaves, pedicels and calyx lobes, more deeply cleft corolla, and especially by the puberulous filaments.

RUBIACEAE

(P. C. Standley, Chicago)

RUDGEA **isthmensis** Standl., sp. nov. Arbuscula 4-metralis ut videtur omnino glabra (flores non visi), ramis gracilibus viridibus teretibus, internodiis valde elongatis; stipulae deciduae, non visae, basi intus setis numerosis incrassatis corneis pallidis ca. 2 mm. longis persistentibus auctae; folia mediocria breviter petiolata chartacea, petiolo crassiusculo 8–11 mm. longo; lamina ovata vel oblongo-ovata 12–14 cm. longa 5–7.5 cm. lata anguste longiacuminata, basi obtusa vel rotundata atque breviter contracta, supra opaca viridis, nervis venisque prominulis, subtus fere concolor subflavescens, costa elevata, nervis lateralibus utroque latere ca. 8 prominentibus angulo latiusculo adscendentibus subarcuatis remote a margine conjunctis, venulis prominulis laxe reticulatis, axillis nervorum lateralium poro magno domatiatis; inflorescentia terminalis parva cymoso-paniculata ca. 2.5 cm. longa et 3 cm. lata pauciflora 18 mm. longe pedunculata, ramis primariis basi non bracteatis, infimis divaricatis rigidis, floribus sessilibus; fructus late ovalis 1 cm. longus 8 mm. latus, pyrenis dorso grosse obtuse costatis.—CANAL ZONE: vicinity of Salamanca Hydrographic Station, Río Pequení, alt. 80 m., July 28–29, 1938, *Woodson, Allen & Seibert 1618* (Herb. Field Mus., TYPE; duplicate in Herb. Missouri Bot. Garden).

The only other species of *Rudgea* previously known from the region, *R. cornifolia* (Humb. & Bonpl.) Standl. *(R. fimbriata* Standl.) has practically sessile leaves. In *R. isthmensis* the remains of the calyx persistent upon the fruit show that the calyx is barely 0.5 mm. in height and remotely denticulate.

CAPRIFOLIACEAE

Viburnum stellato-tomentosum (Oerst.) Hemsl.—chiriquí: thickets between Finca Lérida and Boquete, ca. 1300–1700 m., July 8–10, 1938, *Woodson, Allen & Seibert 1103.* This species, apparently rather frequent in Costa Rica, has previously been unrecorded from Panama.

CUCURBITACEAE

Cucurbitacea sp. We have been unable to place this specimen either to genus or to species. Our material consists of a rather slender, scandent herb; stems essentially glabrous; leaves ovate, broadly cordate, acutely acuminate, 12–13 cm. long, 10–11 cm. broad, membranaceous, minutely and sparsely bullate, otherwise glabrous, the petioles very slender, 4 cm. long, glabrous; tendrils opposite the leaves; staminate inflorescences spicate-paniculate, in some cases with as many as 6 slender branches 15–30 cm. long, bearing occasional reduced tendrils interspersed amongst the distant, nearly sessile floral clusters; staminate flowers greenish-yellow, pedicel 1 mm. long; calyx-lobes 5, equal, broadly ovate, 2.5 mm. long; corolla a fleshy, entire, disc-like ring 0.5 mm. deep, adnate to the base of the calyx; staminal column slender, 1 mm. long, anthers sessile, 5, sigmoid. Since pistillate flowers and fruit are lacking, it is scarcely possible to refer the material to either a new or a pre-existing genus.—bocas del toro: vicinity of Nievecita, alt. ca. 0–50 m., Aug. 8–19, 1938, *Woodson, Allen & Seibert 1841* (unicate, in Herb. Missouri Bot. Garden).

COMPOSITAE

(S. F. Blake, Washington; Senecio by J. M. Greenman, St. Louis)

Senecio Cooperi Greenm.—chiriquí: Bajo Mona, mouth of Quebrada Chiquero, along Río Caldera, alt. 1500–2000 m., July 3, 1938, *Woodson, Allen & Seibert 1014.* Previously known only from the highlands of Costa Rica.

Lagenophora **panamensis** Blake, sp. nov. (pl. 23). Herba perennis pumila pluricaulis; caules adscendentes ca. 1 dm. alti sparsissime pubescentes usque ad capitula foliosi; folia basalia spathulata v. oblanceolata ca. 5 cm. longa obtusa penni-

nervia subcoriacea, lamina crenato-serrata breviter ciliata caeterum subglabra in petiolum subaequalem late marginatum sparse ciliatum angustata; folia caulina ca. 9–14 internodiis saepius longiora, inferiora basalibus similia sed breviora, media et superiora linearia sessilia sparse ciliata prope apicem crenato-serrata, suprema integra; capitula 2–3 parva radiata terminalia et in axillis supremis, pedunculis dense adscendenti-pilosulis quam foliis subtendentibus brevioribus; involucri ca. 4 mm. alti 3-seriati paullum gradati appressi, phyllaria lineari-oblonga obtusa tenuiter subherbacea angustissime subscarioso-marginata 1-nervia infra ciliata supra ciliolata; radii numerosi patentes parvi lavendulacei; corollae disci flavae (?); achenia radii obovata margine crasse nervata breviter rostrata, rostro dense sessili-glanduloso; achenia disci similia, rostro brevissimo annulari; pappus nullus.

Plant apparently cespitose; rootstock oblique, about 4 mm. thick; stems several, greenish, subterete, few-ribbed, essentially glabrous below, above sparsely puberulous and with scattered long hairs, leafy throughout; basal leaves few, about 5 cm. long including petiole, the blade 2–2.8 cm. long, 10–12 mm. wide, crenate-serrate throughout (teeth 5–8 pairs, rather crowded, 1–3 mm. long, obtusely callous-pointed at the rounded apex, occasionally 1-toothed on the side), short-pilose-ciliate, narrowed into the petiole, this sparsely pilose-ciliate with longer hairs especially toward base; middle stem leaves 1.5–2.5 cm. long, 3–5 mm. wide, sparsely pilose-ciliate with many-celled hairs, toward apex crenate-serrate or serrate with 1–4 pairs of obtuse or acute teeth; peduncles about 5 mm. long; heads (moistened) 12.5 mm. wide; disk (moistened) about 8 mm. wide, 4 mm. high; involucre flattish-hemispheric, about 9 mm. wide, 4 mm. high, the phyllaries 0.6–0.8 mm. wide, sometimes purplish-tinged above, sparsely pilose-ciliate toward base, more densely ciliolate toward tip with sometimes subglandular hairs, otherwise glabrous; disk flattish, naked; rays about 57, spreading, 2-seriate, fertile, "pale pink-lavender," glabrous, the tube 0.3 mm. long, the lamina narrowly oblong or linear-elliptic, 2-dentate or 3-denticulate, 2–3-nerved, 2.6–2.8

mm. long, 0.6–1 mm. wide; disk flowers about 28, apparently mostly sterile but some perhaps fertile, their corollas glabrous, 2.2–2.5 mm. long (tube 0.6–0.8 mm., throat campanulate, 0.7–0.9 mm., teeth 5, ovate, acute, spreading, 0.8 mm. long); ray achenes (immature) obovate, compressed, thick-nerved on the margin, nerveless on sides, 2.2 mm. long including beak, abruptly or gradually narrowed into a short thick densely sessile-glandular neck 0.4 mm. long, otherwise glabrous, epappose; disk achenes (immature) obovate, compressed, thick-nerved on margin, nerveless on the sides, 2 mm. long, 0.7–0.8 mm. wide, slightly narrowed at apex and then slightly expanded into a ring-like usually densely sessile-glandular neck about 0.1 mm. high; style branches of hermaphrodite flowers lance-oblong, acute, hispidulous throughout dorsally, without stigmatic lines.—CHIRIQUÍ: on potrero, Loma Larga to summit, Volcán de Chiriquí, alt. 2500–3380 m., July 4–6, 1938, *Woodson, Allen & Seibert 1047* (U. S. National Herb., no. 1,746,842, TYPE).

The discovery of a species of *Lagenophora* on the highest mountain in Panama is of considerable phytogeographic interest. *Lagenophora,* a genus of Astereae containing about twenty-three species, has its center of distribution in the Australian region. Seven species are found in New Zealand and outlying islands, and four others in Australia, one of which occurs also in Ceylon, eastern India, Hongkong, Java, Sumatra, and the Philippines. Three species have been described from the Hawaiian Islands, two from the Liukiu Islands, and one each from Borneo, New Caledonia, and the Fiji Islands. The half dozen proposed species from South America reduce to three, *L. harioti* Franch., *L. hirsuta* Less., and *L. nudicaulis* (Lam.) Dusén (*L. commersonii* Cass.), which range from central Chile (Rancagua) to Tierra del Fuego, one of them occurring also on Tristan da Cunha. *L. purpurascens* Phil. is reduced to *L. nudicaulis* by Reiche, and *L. lechleri* and *L. muscicola,* both *nomina nuda* made by Schultz Bipontinus, are equivalent to *Laestadia lechleri* and *L. muscicola* of Weddell.

The three South American species are all scapose or essen-

tially so and quite different in appearance from *L. panamensis.* Of the some fourteen species available for comparison, the Hawaiian *L. mauiensis* Mann is most similar in appearance to *L. panamensis,* but the former is readily distinguished by its serrate rather than crenate leaves, its glandular-pubescent stem, and its much larger solitary heads.

Sabazia triangularis var. **papposa** Blake, var. nov. Achenia radii glabra epapposa vel interdum squamellam unicam oblongam fimbriatam 0.6 mm. longam angulo interno gerentia; achenia disci erecto-hirsutula papposa; pappi squamellae 5–6 1-seriatae oblongae obtusae fimbriatae 0.8 mm. longae tubam corollae aequantes.—chiriquí: Loma Larga to summit, Volcán de Chiriquí, alt. 2500–3380 m., July 4–6, 1938, *Woodson, Allen & Seibert 1055* (U. S. National Herb., no. 1,746,843, type).

In the type of *Sabazia triangularis* Blake *(Pittier 3109,* El Potrero Camp, Volcán de Chiriquí, alt. 2800–3000 m.) the ray achenes are glabrous and epappose, the disk achenes hispidulous and likewise epappose. The differences between the typical form and the variety are much like those separating *Sabazia pinetorum* Blake and its var. *dispar.*

Piqueria trinervia Cav. var. luxurians Kuntze—chiriquí: Loma Larga to summit, Volcán de Chiriquí, alt. 2500–3380 m., July 4–6, 1938, *Woodson, Allen & Seibert 1044.* Apparently the first record for any form of the genus in Panama. The variety was previously known from Costa Rica; the typical form ranges from Mexico to Costa Rica, and is also recorded by Robinson from Haiti.

Explanation of Plate

PLATE 20

Vriesia Woodsoniana L. B. Smith

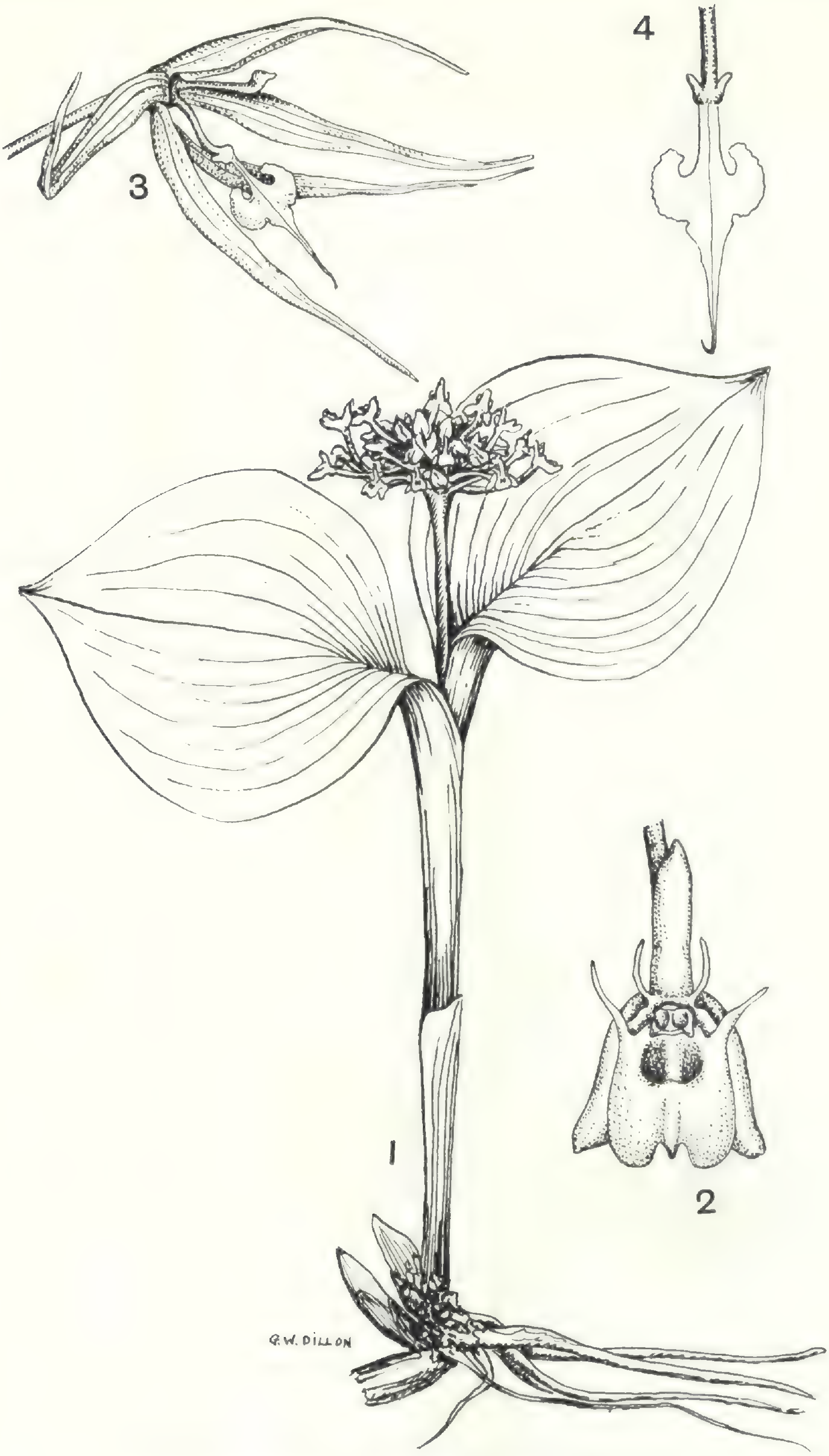
WOODSON AND SEIBERT—FLORA OF PANAMA

Explanation of Plate

PLATE 21

1. *Malaxis Woodsonii.* Plant natural size.
2. *Malaxis Woodsonii.* Flower × 5.
3. *Notylia Cordesii.* Flower × 4.
4. *Notylia Cordesii.* Labellum × 8.

(Figures drawn from the types by G. W. Dillon.)



WOODSON AND SEIBERT—FLORA OF PANAMA

EXPLANATION OF PLATE

PLATE 22

Maytenus Woodsoni Lundell. From type specimen, *Woodson, Allen and Seibert 1065,* in Herbarium of the University of Michigan. × ½.

WOODSON AND SEIBERT—FLORA OF PANAMA

EXPLANATION OF PLATE

PLATE 23

Lagenophora panamensis Blake (natural size).

WOODSON AND SEIBERT—FLORA OF PANAMA

THE GENETIC COEFFICIENTS OF SPECIFIC DIFFERENCE

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For the precise study of evolution of populations, races, or species, nearly every problem sooner or later requires some measurement of the morphological divergencies in the groups under observation. This is equally true and the problem is fundamentally the same whether one be studying very closely related species of *Drosophila* (Dobzhansky and Mather, '39), varieties of gall wasps (Kinsey, unpublished), fields of irises (Anderson, '36a), or the races of man (Pearson, '26, and various other authors). It is usually taken for granted in such studies that any measurable feature or features of the organism will serve equally well as a measure of likeness if only the records be made with care and treated with the precise methods of biometry. Improvements have recently been made by considering differences in groups of measurements, the data being combined crudely (Anderson, '36a, '36b, Anderson and Hubricht, '38) or by refined biometrical techniques (Fisher, '36b).

These methods are all based on the tacit assumption that species differences are expressed more or less at random. A study of such differences has convinced us that their morphological nature renders these methods relatively inefficient. Species do not differ in a random manner. They differ in a peculiar and subtle way. If any two closely related species of the flowering plants are examined critically it will be found that they differ as a whole by two sets of harmonically integrated tendencies (Anderson and Whitaker, '34). Such a conclusion, however, is of little use in quantitative work. In section I, therefore, there is developed a precise mathematical

expression for the difference between "two sets of harmonically integrated tendencies." The application of this formula is illustrated in section II, where an attempt is made to analyze the differences between *Nicotiana alata* and *N. Langsdorffii* and to show how, from an estimate of their "genetic co-efficients," an efficient measure of their total difference could be developed.

I. A GENERAL FORMULA FOR THE EFFICIENT MEASUREMENT OF SPECIFIC DIFFERENCES

It might seem impossible to formulate any mathematical definition of species differences broad enough to apply to organisms as different as flowering plants, insects, and vertebrates. A little reflection, however, will remind one that the gene-chromosome-cell relation is fundamentally the same in these various organisms and that species differences, in so far as they rest on the gene-chromosome-cell system, may be expected to exhibit certain general features.

Closely related species or races may be conceived as made up of a large number of characters, the number considered in any particular instance depending upon the viewpoint of the observer. Any two closely related species, however, will have the same sets of characters which differ only in their proportionate development. In studying races of mankind, for instance, there might be considered the head, the neck, the trunk, the arms, and the legs of the two races. If the set of characters were subdivided into such categories as fingers, ears, etc., it would still be possible to observe the same set in both races.

We may therefore define the gross morphology of any organism as being the sum of a set of characters: Organism = A + B + C + D + E + F + ... + N. In so far as species differences rest in the germ-plasm, the basic differences between the two species will not be differences in these characters but in the germ-plasm which give rise to them, and they can be thought of as made up of a set of differences between corresponding factors of the germ-plasm. These factors in the germ-plasm we shall write a, b, c, d, e, ... n for one species, and a′, b′, c′, d′, e′, ... n′ for the other. Some of these may relate to proc-

esses so general that they are expressed in every character (as, for instance, a gene affecting cell division or wall formation). For such factors we shall use the first letters of the alphabet and we may write the first species as: (abc ......)A + (abc ......)B + (abc ......)C + (abc ......)D + ... + (abc ......)N, while the second species will be written: (a′b′c′ ......)A + (a′b′c′ ......)B + (a′b′c′ ......)C + (a′b′c′ ......)D + ... + (a′b′c′ ......)N. The dots within the parentheses represent additional factors affecting all the characters. Other factors will affect only similar characters, as, for instance, the leaf and the calyx in flowering plants, or hand and foot in vertebrates. For them we may use the middle letters of the alphabet. There are probably also elements in the germplasm which affect only single characters. If we use letters at the end of the alphabet for them, then the total morphological difference between two related species is described by the following mathematical expression:

(abc ... m .. x ..)A + (abc ... m .. y ..)B + (abc ... n .. z ..)C + ... + (abc ... p .. w ..)N − (a′b′c′ ... m′ .. x′ ..)A + (a′b′c′ ... m′ .. y′ ..)B + (a′b′c′ ... n′ .. z′)C + ... + (a′b′c′ ... p′ .. w′ ..)N.

From this it follows that a set of observations upon A or upon A and B will probably be an inefficient way of getting at fundamental differences between the two species. That is to say, instead of comparing two races of men by their skulls alone, or two species of *Acer* by their leaves, we should first attempt to determine the most efficient way of measuring the coefficients which affect skull, trunk, and appendages in man, or leaf, stem, and inflorescence in *Acer*. What is needed is the most efficient way of measuring (a − a′), (b − b′), (c − c′), ... (n − n′). These genetic coefficients of specific difference (a vs. a′, b vs. b′, c vs. c′, etc.) cannot be determined from casual inspection. While their determination is a much more simple matter in the flowering plants than in the insects or vertebrates, it will even there require detailed observation and experiment. How to measure any particular specific difference is a research problem which should be undertaken before one proceeds to the actual measurement.

II. AN ESTIMATE OF THE GENETIC COEFFICIENTS WHICH DIFFERENTIATE *NICOTIANA ALATA* FROM *N. LANGSDORFFII*

The species chosen for comparison were *Nicotiana alata* and *N. Langsdorffii.* They were selected because (1) they are easily grown for observation and experiment, (2) a large body of genetic and cytological data is already at hand concerning their behavior in crosses and back-crosses (East, '16, Sachs-Skalinska, '21, Brieger, '35, Smith, '37, Avery, '38, Anderson, '39), (3) an estimate of their genetic coefficients was desired as the basis for analysis in further crosses. *Nicotiana alata* is the night-blooming species with large white flowers, known to gardeners as *N. affinis.* *N. Langsdorffii* is a smaller, chunkier species, with bright green flowers and blue pollen. Representative flowers of each are illustrated in plate 24, A–C. Seed of *N. alata* was obtained from the Palmer Seed Company of St. Louis. Some of the plants bore pale pink corollas, probably the result of hybridization in cultivation with X *Nicotiana Sanderae (= N. alata X N. Forgetiana).* The strain of *N. Langsdorffii* was kindly supplied by Dr. H. H. Smith of the U. S. Department of Agriculture. The known facts of the relationship and distribution of the two species have been summarized by Avery ('38). The points which concern us here are that both species are diploid members of the 9-chromosome group of *Nicotiana,* and that they are both native (or are at least widely distributed) in a large region in central South America. From a study of the meiotic configurations of their hybrids Avery concluded that the gross differences in their chromosome complements were confined to two translocations in three pairs of chromosomes. Like some of the evidence submitted below, this fact supports (though it does not prove) Anastasia's speculation ('14) that *N. Langsdorffii* may be the result of a cross between *N. alata* or a closely related species and some such member of the 24-chromosome group as *N. rustica,* by which a few segments of *rustica* germ-plasm became incorporated in an *alata* genom (Avery, '38). If this is indeed the relationship between *N. alata* and *N. Langsdorffii,* the case, while exceptional, is not unique in our opinion. There

are a number of genera of flowering plants in which the morphological resemblances between the species would indicate similar relationships.

1. Cell size.—In searching for the fundamental genetic coefficients which differentiate these two species, one of the most obvious places to look is the cell itself. If there are outstanding differences in cell size, cell uniformity, or in the development of the cell wall, they should be comparatively easy to detect. An inherent cell-size difference, for instance, should manifest itself in a consistently larger size of one species, even in those organs in which there are no obvious differences in proportion. Even a superficial examination will show that

Fig. 1. A, corolla-tube of *Nicotiana alata* (above) and of *N. Langsdorffii* (below); B, corolla-throat of *N. alata* (above) and of *N. Langsdorffii* (below). All figures drawn to the same scale.

Nicotiana alata is generally larger throughout than is *N. Langsdorffii.* The shape differences in the corolla are confined to the base of the tube and the limb. The throat of the corolla, although complex in shape, is of practically the same proportion in the two species, and is roughly half again to twice as large in *N. alata* as in *N. Langsdorffii* (pl. 24, and fig. 1, B). The pedicels, the cross-section of the style, the capsule, and the seeds show the same relationship. Histological examination shows that the surmise of a fundamental difference in cell size is probably correct. While measurements of whole tissues were not undertaken, examinations were made in all those organs which seemed to have about the same proportions. Camera-lucida drawings are presented in fig. 2. It will be noted that, in each, the cells of *N. alata* are larger than those of *N. Langsdorffii* and that in each the ratio of their diameters

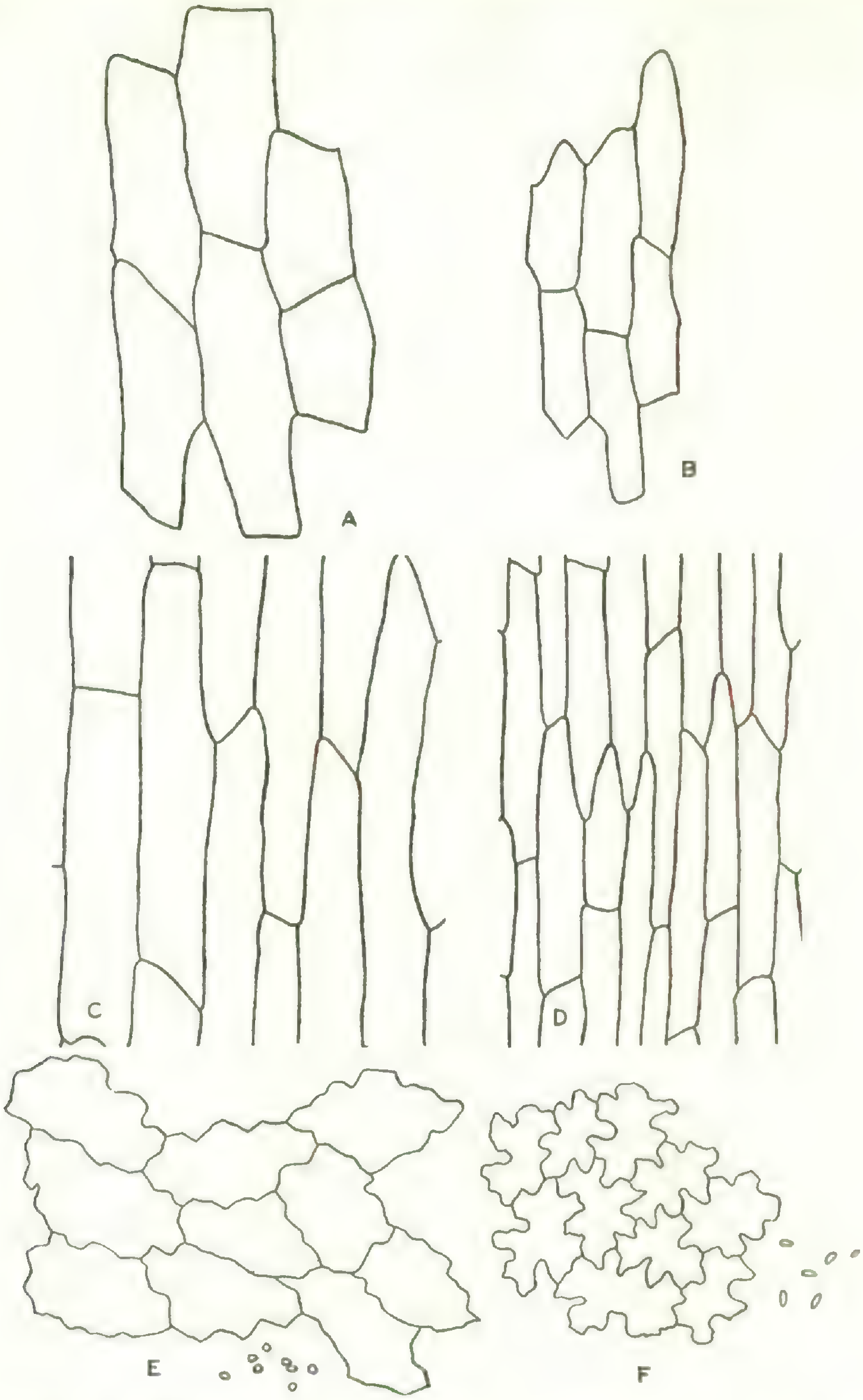
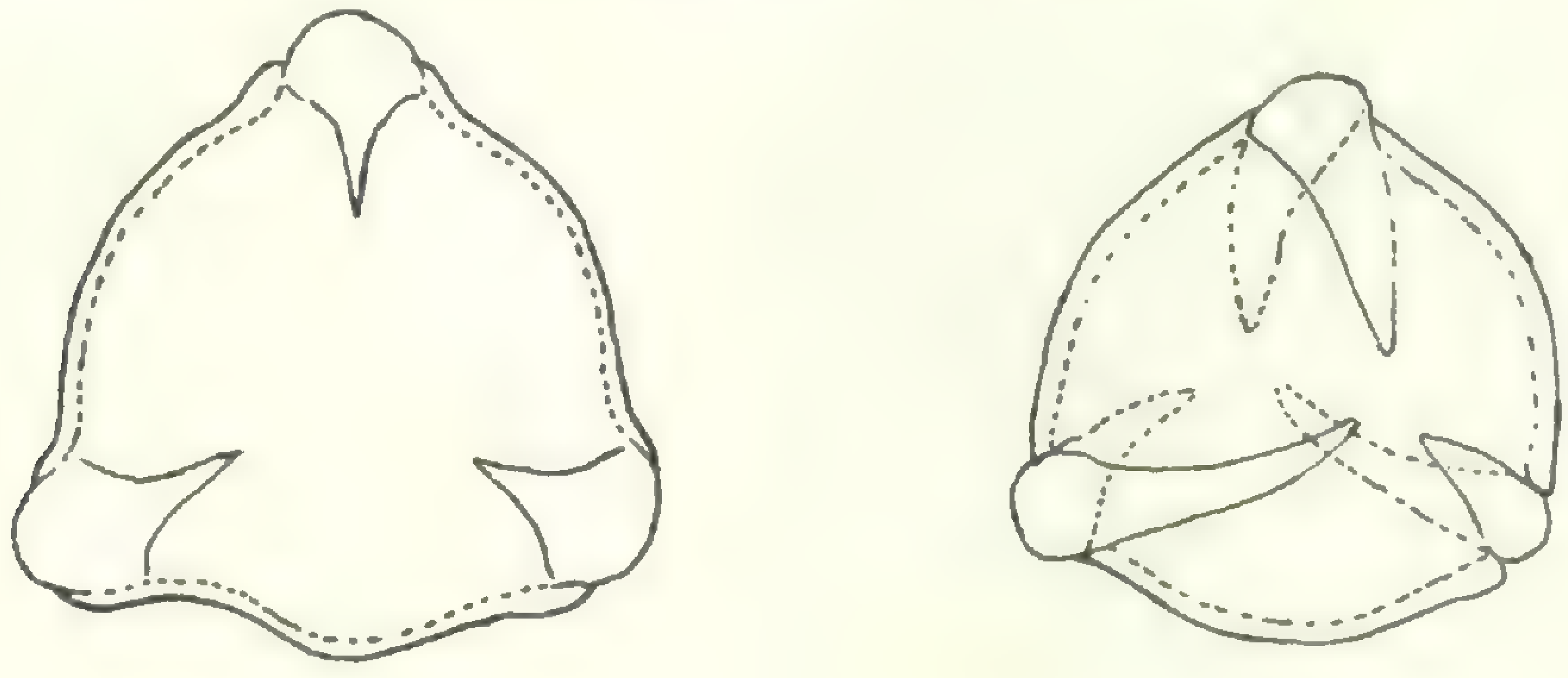


Fig. 2. Histological details to show relative size of cells in *Nicotiana alata* and *N. Langsdorffii*: epidermal cells from base of corolla-tube, (A) in *N. alata*, (B) in *N. Langsdorffii*; epidermal cells from corolla-throat, (C) in *N. alata*, (D) in *N. Langsdorffii*; ten epidermal cells from corolla-limb, (E) in *N. alata*, (F) in *N. Langsdorffii*. The plastids drawn in E and F show relative size, but not relative number or distribution.

is roughly from 1:1.5 to 1:2. Furthermore, this ratio agrees with the size differences of the organs concerned. Note particularly the pedicels, the corolla-throats, the pollen, and the seeds (fig. 3 and pl. 24).

As a working hypothesis we may therefore conclude that one of the fundamental differences between *N. alata* and *N. Langsdorffii* is cell size, and that it is apparently expressed throughout the organism. Its expression is certainly modified by localized differences in cell elongation, as will be shown below, and perhaps by differences in cell number, though we have as yet little definite information on that point.



A B

Fig. 3. Pollen grains of (A) *Nicotiana alata,* and (B) *N. Langsdorffii.*

2. *Cell elongation.*—The most striking difference in flower shape between the two species is the constricted portion of the corolla-tube below the point where the stamens are inserted. In *Nicotiana Langsdorffii* this is so short that it cannot be seen without removing the calyx. In *N. alata* it is much longer than the throat (pl. 24, A, C, and fig. 1, A). Histological examination showed that the difference is mainly due to cell elongation. Allowing for the basic difference in cell size (see above) the cells of the tube in *N. alata* are proportionately no wider than those in *N. Langsdorffii* though they are many times as long (Nagel, '39). It seemed probable that such a difference should be expressed elsewhere throughout the plant, and even a cursory examination showed this to be the case. *Nicotiana alata* is not only a somewhat larger plant

than *N. Langsdorffii;* it has a general tendency to be somewhat more elongated. It has narrower leaves (largely due to more elongated petioles), longer internodes, narrower bracts, longer calyx-lobes, a much longer style, and a more pointed ovary, resulting in elongate lobes of the ripened capsule (pl. 24, D, E). It seemed probable that all of these correlated differences rest on a difference in the mechanism of cell elongation. This point has very kindly been investigated by Miss Nagel, whose results are reported in the accompanying paper. She finds that there is a basic difference in the auxin response of the two species. *Nicotiana Langsdorffii* apparently inactivates auxin very readily and therefore shows little or no response even when it is supplied artificially in various ways. *Nicotiana alata,* on the other hand, does not inactivate it so readily and, in stem, leaf, and flower, shows even greater elongation when additional auxin is supplied artificially. It therefore seems quite definitely established that one of the differentiating genetic coefficients affects the auxin mechanism, probably by bringing about greater auxin inactivation in one species than in the other.

It seems quite probable that several of the coefficients listed below may be only accessory manifestations of this same auxin difference. This is particularly true of number 3, geotropic response, and number 4, leaf-vein angles.

3. Geotropic orientation of appendages.—Appendages of the axis, and its own branches, diverge at a more acute angle in *Nicotiana alata* than in *N. Langsdorffii.* This angle divergence is roughly the same in leaves, pedicels, bracts, and branches of the inflorescence (fig. 4). It has been well established that the geotropic response of flowering plants is accomplished through auxin regulation (Dolk, '36). Whether or not the difference in appendage orientation is due to the same auxin-mechanism difference as that affecting corolla-tube elongation we have as yet no means of proving.

4. Leaf-vein angles.—The angles made by the side-veins with the midrib of the leaf are also more acute in *N. alata* than

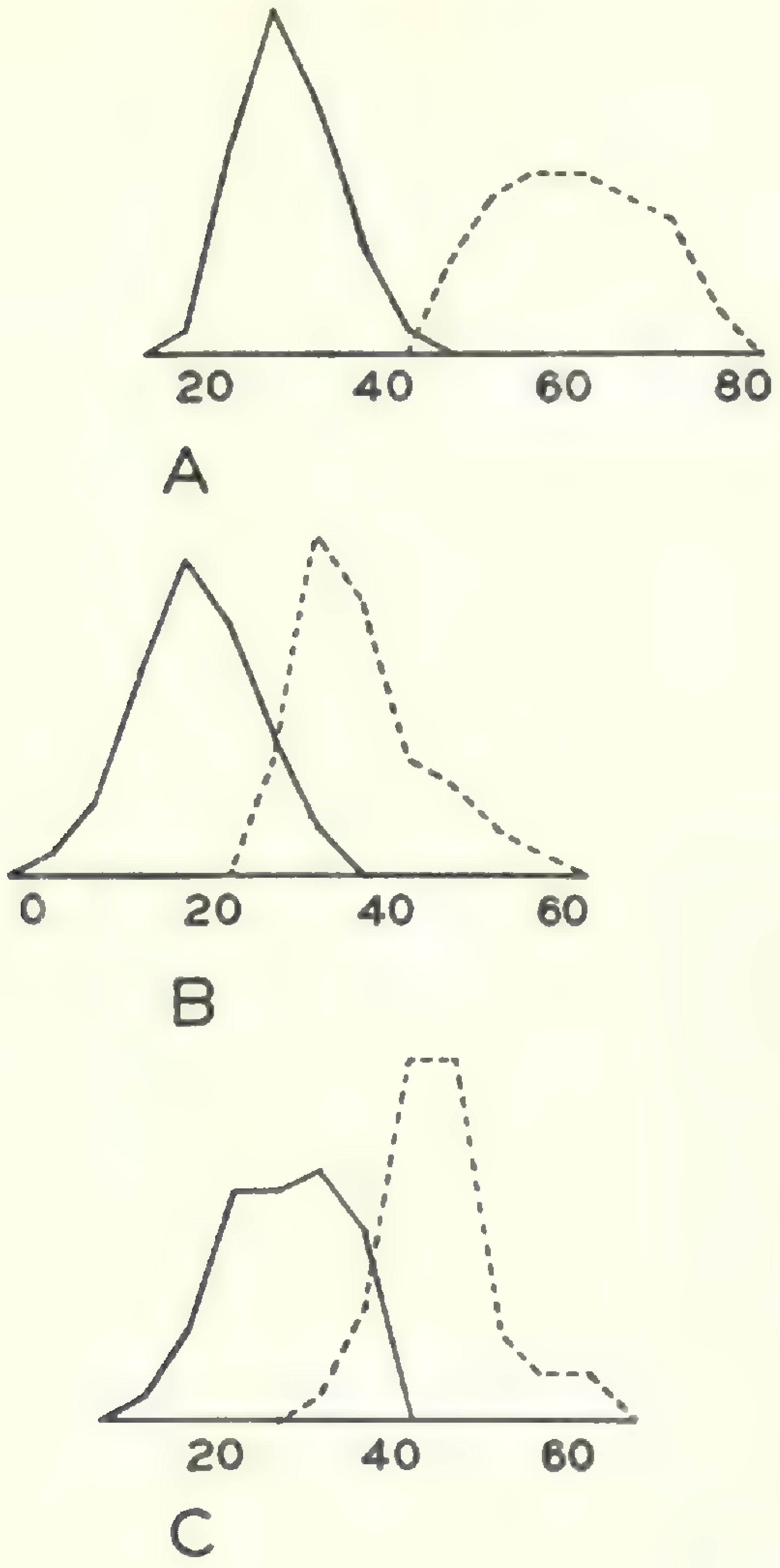


Fig. 4. Frequency distributions showing angle of divergence of (A) leaf, (B) flowering pedicel, and (C) branch of the inflorescence. The solid line, in each case, represents *Nicotiana alata,* the broken line, *N. Langsdorffii.* The numbers along the base lines represent the angles of divergence, in degrees.

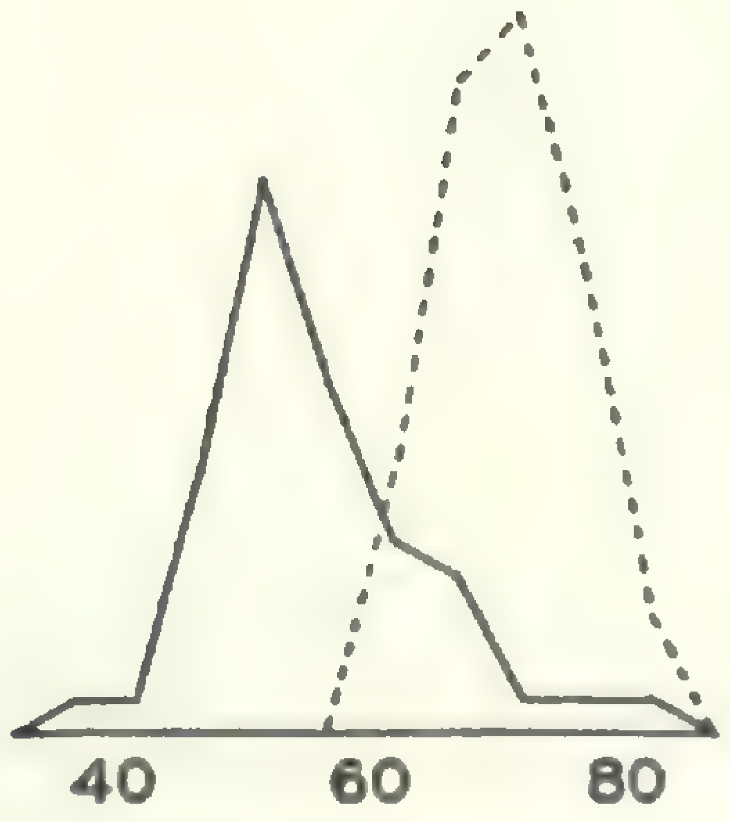


Fig. 5. Frequency distributions showing angle of divergence of the secondary vein near the base of the leaf blade, in *Nicotiana alata* (solid line) and *N. Langsdorffii* (broken line). The numbers represent the angles, in degrees.

in *N. Langsdorffii* (fig. 5). While it is probable that this difference is related to auxin concentrations, further experimentation will be required to discover its relation to geotropism and elongation in the appendages.

5. *Plastid color.*—The most conspicuous difference between the two species is the color of the flowers. The corollas of *N. alata* are a clear ivory-white within, somewhat tinged with green on the outside. Those of *N. Langsdorffii* are bright green

on both sides. Microscopical examination shows this difference to reside in the plastids, which are ivory in the former and green in the latter. While this difference is most extreme in the flower it is also expressed in other parts of the plant, notably in the midribs of the leaves and in the pedicels. These are ivory at maturity in *N. alata* and green in *N. Langsdorffii.* We therefore conclude that one of the genetic coefficients which differentiate the two species is the ability to develop ivory rather than green plastids under certain conditions.

6. *Peripheral foliar development.*—One of the most striking differences between the flowers of *N. alata* and *N. Langsdorffii* occurs in the corolla-limb. In the former species it is larger and deeply lobed; in the latter, small and almost unlobed. The difference in cell size, discussed above, would account for not more than half of the difference in limb size. That there is evidently a genetic coefficient in *N. alata* producing continued development of the marginal tissue in foliar organs is suggested by a comparison of the leaves of the two species. Those of *N. Langsdorffii* are characteristically flat. In those of *N. alata* the margin has developed to such an extent that it cannot be accommodated in a flat position and is strongly waved. We therefore suggest that one of the differentiating genetic coefficients we are seeking affects the development of the margin in leaf and corolla.

7. *Basal foliar development.* A further conspicuous difference between the species is in the shape of the corolla limb, which is deeply lobed in *N. alata* and so slightly lobed in *N. Langsdorffii* that the limb sometimes has a slightly greater diameter at the sinuses than at the apex (which can still be recognized, however, by the veining pattern). Part of this difference in shape is a physiological necessity of the greater size and is not due to specific shape differences. It has already been shown (Anderson, '39) that in the genicly uniform F_1 between the two species there is a correlation of .3105 ± .1077 between the degree of lobing and the limb width. An examination of the limb offers a simple explanation of this correlation.

The main vein is down the center of the lobe, and it might be expected that with increased growth of the limb there must of necessity be a greater increase proportionately at those points near the food supply (the tips of the lobes) than at those points which are remote from the food supply (the sinuses). There is evidence, however, that there are factors in *Nicotiana alata* making for accentuated lobes other than those concomitant with the increase in size. The F_2 correlations between lobing and limb width are much greater (.7186 ± .0300) than those of the F_1, indicating a genetic correlation as well as a purely physiological one. Furthermore, second-generation hybrids with limbs of the same size differ among themselves in the amount of lobing of the corolla. *Nicotiana alata* therefore differs from *N. Langsdorffii* not only in the size of its limb but in a tendency for the limb to grow more towards the tip and less towards the base.

It seems not impossible that this same tendency may also operate in the other foliar organs. The leaves of the two species differ in length of the petiolar portion (as has been discussed above) and in shape of the basal portion of the blade, which is proportionately wider in *N. Langsdorffii.* If two leaf blades of about the same size and age are selected and laid side by side it will be seen that their tips are very similar and that most of the difference in blade shape is due to the wider base. The leaf of *N. Langsdorffii* is furthermore more decurrent on the stem than is that of *N. alata.* As a basis for further experiment we would therefore suggest that one of the genetic coefficients distinguishing the two species is a factor for greater basal development in foliar organs. Its chief effect in *N. Langsdorffii* is to make the blade proportionately broader at the base and, by exerting a similar effect upon corolla-lobes, to lessen the lobing of the corolla. The evidence for such a coefficient is much more speculative than that for the coefficients previously discussed.

8. *Pollen color.*—The pollen of *N. Langsdorffii* is bright blue, that of *N. alata* is ivory-colored. Smith has shown ('37) that the production of blue pollen is due to two complementary

genes which are independent of the gene for green plastid color.

9. Time of blooming.—The flowers of *N. alata* begin to open late in the afternoon and close, as if wilted, during most of the day. While we have made no precise experiments, this is apparently correlated with both light and temperature. On a dark day, or indoors, the flowers of *N. alata* may remain more or less expanded throughout the day. *Nicotiana Langsdorffii*, on the other hand, is a day-blooming species, though it wilts in strong sunshine even more readily than other day-blooming Nicotianas. It seems possible that this difference between the species may be another expression of the plastid difference discussed above. If this be true, it should be possible to establish the fact by a careful study of second-generation and back-cross individuals.

10. Scent.—The flowers of *N. alata* are delightfully scented, particularly when they first expand in the early evening. Those of *N. Langsdorffii* have little or no odor.

11. Inflorescence.—Typical inflorescences of each species are diagrammed in fig. 6. They exhibit at least two kinds of difference between the two species: degree of branching, and determinate vs. indeterminate nodes. *Nicotiana Langsdorffii* shows a much higher degree of branching than does *N. alata.* It is difficult to score definitely because in both species the amount of branching is affected by the food supply. Starved in a two-inch pot even *N. Langsdorffii* will have a simple stem. When grown in four- or five-inch pots, however, it always shows numerous well-developed secondary axes and at least a few of the third and fourth order. *Nicotiana alata* often shows only a few secondary and no tertiary axes.

Nicotiana alata is apparently indeterminate, but there is no transparent relation between flowers and bracts. In *N. Langsdorffii* every axis, whether primary, secondary, or of a higher order, is terminated by a flower. The terminal flower on the primary axis is the first to bloom, followed by those terminating the two upper secondary axes. These facts would indicate that the inflorescence is in part truly determinate. On

the other hand, these terminal flowers are not subtended by bracts, but small bracts, usually without flowers, occur a short way up each of the secondary axes. This might indicate that the terminal flowers are falsely determinate. Whether the de-

Fig. 6. Inflorescence diagrams of (A) *Nicotiana alata,* and (B) *N. Langsdorffii.* The angles of divergence of leaves, pedicels, and branches are average ones for the two species. No attempt is made to show relative length of internodes, leaves, or pedicels. Broken lines indicate continuation of the axes.

terminateness of *N. Langsdorffii* is affected by coefficients which are expressed elsewhere in the organism cannot be ascertained without further experiment. From what is known about such matters it would seem highly possible that the degree of branching might be affected by the auxin mechanism.

Cell shape.—There are various differences in cell shape between the two species, particularly in the cells of the epidermis. Not enough work has been done to show whether or not these differences can be reduced to differences in one or a few basic coefficients.

Zygomorphy.—The flowers of both species are slightly zygomorphic, though in *N. alata* it is the corolla-limb which shows its bilateral symmetry most strikingly, while in *N. Langsdorffii* the expression of this tendency is stronger in the corolla-tube and throat. It is quite probable that these may be further manifestations of the basis for the vein-angle and leaf-angle differences.

In addition to the differences discussed above there are a number of minor ones whose expression is apparently limited to a single organ. Further genetical and physiological experimentation may show that some of these are further effects of the coefficients described above.

TABLE I

SUMMARY OF THE GENETIC COEFFICIENTS DIFFERENTIATING *N. ALATA* FROM *N. LANGSDORFFII*. "x," ORGANS IN WHICH THE ACTION OF THE GENETIC COEFFICIENT IS EVIDENT, "*," THE ORGAN IN WHICH IT CAN PROBABLY BE MEASURED MOST EFFICIENTLY

Genetic coefficients	Vegetative phase		Reproductive phase									Other coefficients of which this may be a further expression
							corolla					
	Axis	Leaf	Axis	Bract	Pedicel	Calyx	Tube	Throat	Limb	Stamen	Pistil	
(1) Cell size	x	x	x	x	x	x	x	*	x	x	x	(2)
(2) Cell elongation	x	x	x	x		x	*		x		x	
(3) Geotropic response	x	x	x	x	*			?	?			(2)
(4) Leaf-vein angles		x							?			
(5) Plastid color		x			x		x	x	*			
(6) Foliar periphery		x		x		x			*		x	
(7) Foliar base		x		x		x			*			(2)
(8) Pollen color										*		
(9) Time of blooming							x	x	*			(5)
(10) Scent							*					
(11) Inflorescence			*									(2)

A tabular summary of the coefficients which we have been able to detect so far is given in table I. It will be seen that eleven different coefficients have been recognized. Further work may possibly add a few more and will probably reduce certain of those listed as separate to a common coefficient. While there may well be differences which are not accounted for by the action of these eleven, they are certainly responsible for most of the total hiatus between the two species.

In this particular problem, as stated above, an estimate of the coefficients was desired as an aid in the genetic analysis. It may be well, however, by way of example, to point out how the estimate might have been used had our concern been the measurement of differences in populations involving the two species. Only two of the coefficients would be difficult to score, (9) and (10). The effects of both of these coefficients are greatly influenced by environmental factors, and it is also difficult to record them objectively. Of the remaining nine, one, (8), is seemingly manifest only in the pollen, and one, (11), only in the branching of the inflorescence. They would obviously have to be measured at those places. Coefficients (1) to (7), however, are all manifest in both the leaf and the flower, and each of the seven is expressed in various other ways. With the above estimate as a guide we should be able to decide where these seven differences might be measured most efficiently.

Were it not for this previous analysis it might have seemed that the leaf is the most promising organ for measurement. It is practically two dimensional, and its characteristics can all be expressed in simple quantitative terms by measuring and counting the veins and the vein angles. The leaf could furthermore be measured on young plants which had not yet reached the reproductive phase. The above analysis demonstrates, however, that the divergence between the two species can much more efficiently be measured in the flower. Though all seven coefficients are expressed in the leaf, its shape is the resultant of four of them, cell size, cell elongation, basal growth, and peripheral growth. Each of these can be determined in the flower with a single measurement, whereas in the leaf the raw

measurements are a complex resultant of all four. Furthermore, nearly all the veins and vein angles would have to be measured and given a thorough statistical treatment before they would be anywhere nearly as useful as the raw data obtained from the flower. The complexities of integrating and interpreting leaf measurements are illustrated in the statistical papers of Czeczott and her associates (Czeczott, '36, Jentys-Szaferowa, '38, Wiśniewski, '32).

The procedure suggested by the above analysis would be much simpler. The seven coefficients could best be measured as follows:

(1) Cell size.—While this is expressed throughout the plant, it can most efficiently be measured in those organs which are not affected by the other coefficients. The diameter of the pedicel or the diameter of the style might perhaps serve but those organs are so small that errors of measurement would be proportionately large. The throat of the corolla (from the insertion of the stamens to the angle marking the limb) is roughly the same proportion in both species (fig. 1, B), its cells seem to be of the same shape, and the limits to be measured are quite definite.

(2) Cell elongation.—This might also be measured in various parts of the plant, or it might even be measured by testing the effect of tissue extracts upon any standardized auxin indicator. The constricted tube of the corolla, however, offers the simplest measurement. In *N. Langsdorffii* it is less than half a cm. long. In *N. alata* it is 6 to 9 cm. While a small portion of this difference is due to (1), the difference in cell size, it is so slight as to be almost negligible by comparison. One measurement on the tube therefore is an almost perfect reflection of the basic difference in cell elongation between the two species.

(3) Geotropic response.—The angle of inclination made by the leaf, the branches of the inflorescence, or the pedicel of the flower might be measured. There is considerable variation among the leaves, however, depending upon the age of the plant, the time of day, the health of the plant, the position with

relation to the rosette, etc. A more comparable measure of (3) can be made by recording the angle made by the pedicel at the time of anthesis.

(4) Leaf-vein angles.—These are easiest to measure on the largest leaves. The best record we have been able to work out is the angle of the first vein above the petiolar portion of the leaf, on the first or second leaf above the rosette (these leaves are often injured, and more consistent results are obtained by choosing arbitrarily the most symmetrically developed of the two).

(5) Plastid color.—While this difference can be seen along the petiole and on the pedicel, particularly in old specimens, it is much more dramatic in the flower. It is there most readily scored on the inside of the flower. As has been previously reported (Anderson, '39), it is easy to recognize three grades of plastid color in the hybrids.

(6) Foliar periphery.—According to the hypothesis suggested above this coefficient accounts for differences in the leaf margin and the floral margin. It would be difficult or impossible to score in the leaf. In the flower it is one of the coefficients responsible for the difference in the width of the limb. The best measurement we have been able to develop so far is the maximum length of the largest corolla-lobe from its tip to the junction with the throat of the tube. This is probably also conditioned by differences in cell elongation and cell size so that a more direct measurement would be preferable.

(7) Foliar base.—Until the operation of the coefficient has been more definitely worked out it is difficult to decide where it might best be measured. For the present we are using the ratio previously adopted (Anderson, '39) for the lobing index (maximum lobe/adjacent sinus).

In the light of our present knowledge the most efficient measure of the divergence between these two species would be based upon the following, as shown in table I: length of corolla-throat, length of corolla-tube, angle between pedicel and axis,

color of corolla, length of corolla-lobe, width of corolla-limb to the sinus, angle of basal leaf vein in first leaf above rosette, color of pollen. It will be noted (table I) that all but one of these can be determined by a single measurement or notation. The original data should then be variously weighted and combined, depending upon the nature of the problem and the use to which the index of specific difference is to be put. Pollen-color and corolla-color differences, for instance, seem to be based on comparatively few genes. In an index designed to be roughly proportional to genic differences, they would be given less weight than measures such as tube length, which are apparently based upon a large number of genes.

It is an interesting fact that, though most of the eleven coefficients are expressed in various parts of the plant, all but one of them are most efficiently measured in the flower. Systematists for two hundred years have emphasized the importance of the flower (and its resulting fruit) in studying relationships between species, genera, families, and orders. It would seem probable that the condition found in these two species of *Nicotiana* must be general among the flowering plants. For reasons whose ontogenetical basis is as yet unknown the germ-plasms of the Angiosperms exhibit their characteristics more conspicuously in the reproductive than in the vegetative phase.

DISCUSSION

A method for the analysis of specific differences through the determination of their genetic coefficients has been developed as a general formula and illustrated by example. Its possible applications are in such different fields that it may be well to indicate three types of problems in which it might be used.

(1) The efficient measurement of specific and subspecific divergence.—The study of evolution by an analysis of variation within and between races and species is older than formal genetics. Until very recently the work of this school has been based on the assumption that if only enough measurements were made and studied with refined mathematical methods,

significant results would emerge. In other words, it was tacitly assumed that organisms vary at random. In our opinion this is putting the cart before the horse. How to measure a specific difference is a research problem which must be undertaken before one takes up the further problem of measuring that difference. As Fisher ('36a) has recently said in discussing the science of craniometry:

> It seems, indeed, undoubtedly true that the theoretical concepts developed . . . have lagged far behind the mass of observational material which has been accumulated. This may be partly due to the sheer magnitude of the programme which the energy of its founders sketched out, partly to an intuitive confidence, widely held in other fields, though everywhere difficult to justify, that, by amassing sufficient statistical material, all difficulties may ultimately be overcome.

The problem of working out even the barest estimate of the genetic coefficients which differentiate the races of men will certainly be much more difficult than the corresponding problem with which we are concerned in *Nicotiana.* Our experience in that latter seemingly unrelated field furnishes a number of suggestions. Biometric study of the races of men has been concentrated upon the skull though our experience with *Nicotiana* suggests that the form of the skull, like that of the leaf, is a complex resultant of many coefficients. It is therefore the worst kind of material for distinguishing between races, since even if there were a clear-cut difference in the basic coefficients separating the races, this would be obscured in its effect on the skull. There seem to be coefficients, for instance, which affect the long bones of the arm and leg in a fairly transparent fashion but cause complex changes in the skull and can be measured there only in an indirect and laborious way. Determinations of variation within and between the races of mankind would yield more significant results if they were based upon records of as many apparently unrelated characters as possible; hair color, hair texture, hair distribution, length of long bones, width of lip, shape of finger nails, finger-print patterns, eye color, and skin color, for instance. An object is much better defined when we describe its weight, color, size, texture, shape, and color pattern than when we have numerous careful

determinations of its weight alone. The latter has until recently been the method of the biometricians.

(2) The genetic analysis of differences between species.—One of the chief sources of evidence for evolutionary changes in the germ-plasm comes from the examination of hybrids between related species. Unfortunately nearly all the evidence which has been accumulated relates to characters rather than to genetic coefficients. To understand what the germ-plasm is doing in a species cross we need to have at least an estimate of the total difference between the parental species and data as to how that total difference is behaving in F_1, F_2, and backcrosses. In most of the published data only one or two obvious differences are followed in this fashion, and even with them the data are reported in terms of such characters as leaf length or plant height. As we have shown above, these characters are the resultants of a number of factors in which the action of any one is very much obscured. If the study of species hybrids could be preceded by at least a rough estimate of the main genetic coefficients which distinguish the parental species, we would have much more direct and dynamic evidence as to differences between related germ-plasms.

(3) The determination of phylogenetic patterns.—If an analysis similar to the one made above could be made for a group of related species it would provide unique data on evolution. While the attempt to consider all the differences between a group of related species in terms of their fundamental coefficients would admittedly be difficult it should not be impossible. Experience with a number of closely related species in several different genera has convinced us that such coefficients as those suggested above operate quite generally among the flowering plants. In *Iris, Acer,* and *Uvularia* closely related species have been found to differ by such general tendencies as absolute cell size, variation in cell size, amount of secondary thickening in cell walls, and geotropic orientation of branches of the axis and of the appendages (Anderson and Hubricht, unpublished). Such a study could most easily be

undertaken in a genus such as *Nicotiana* in which both the leaves and flowers are large and clearly differentiated into definite tubes, limbs, petioles, etc. While it would have to be frankly provisional it would provide a view of phylogeny which would be dynamic rather than static.

SUMMARY

1. From previous studies of closely related species it had been concluded that differences between such species are to be sought not in any one character but in harmoniously integrated tendencies (genetic coefficients) expressed more or less throughout the entire organism. A simple mathematical notation is developed for expressing the resulting morphological hiatus between two species.

2. By way of example, an estimate is made of the genetic coefficients which differentiate *Nicotiana alata* from *N. Langsdorffii.* Eleven such coefficients are suggested, the most important of which affect cell size, plastid development, and the auxin mechanism.

3. Estimates of genetic coefficients might be used in a number of different fields of biology. Their application to the following three problems is discussed: (1) The efficient measurement of specific and subspecific divergence; (2) The genetic analysis of differences between species; (3) The determination of phylogenetic patterns.

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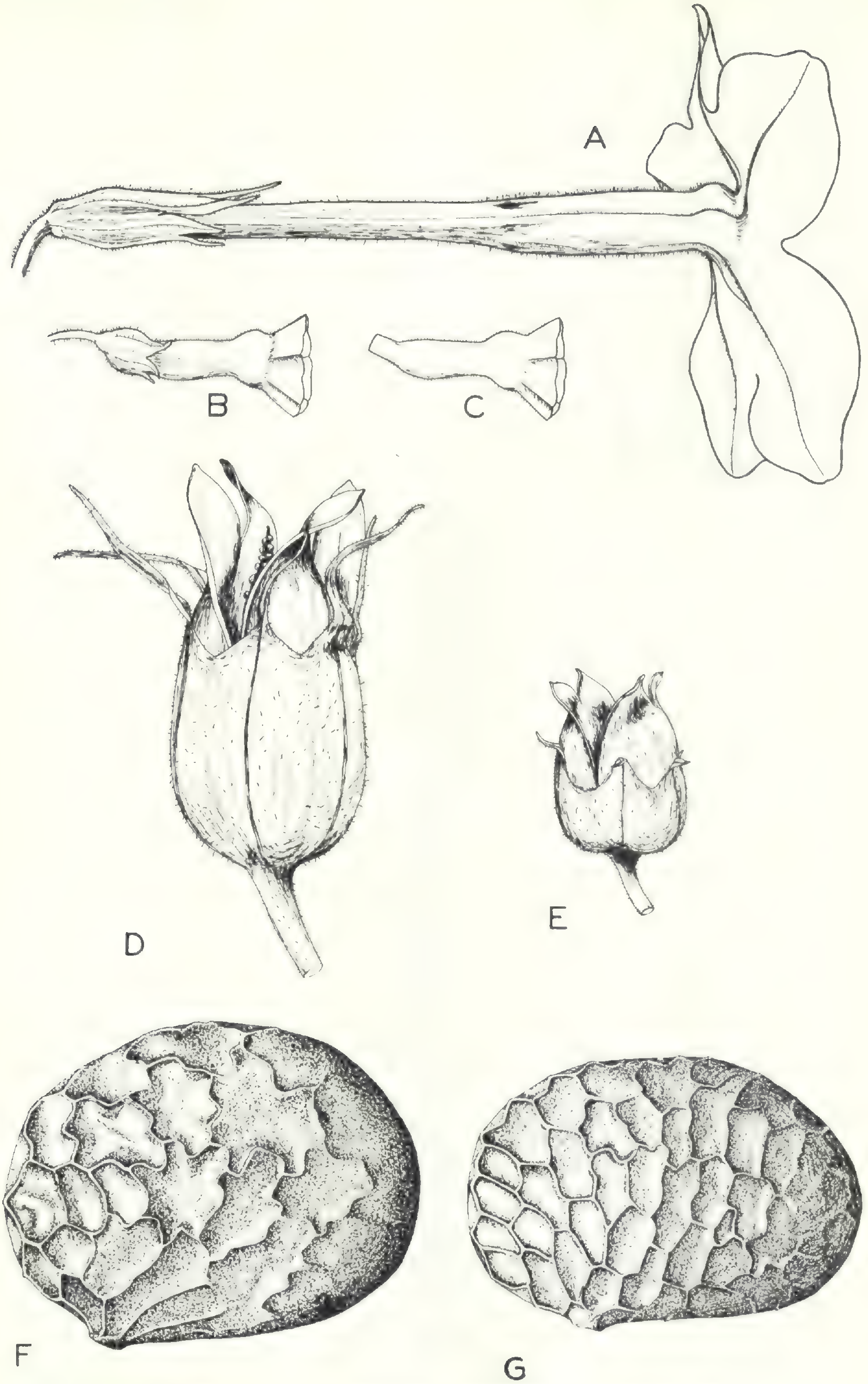
Explanation of Plate

PLATE 24

A. Flower of *Nicotiana alata* (× 7/10).
B. Flower of *N. Langsdorffii* (× 7/10).
C. Same, with calyx removed.
D. Ripe, opened capsule of *N. alata* (× 2).
E. Capsule of *N. Langsdorffii* (× 2).
F. Seed of *N. alata* (× about 50).
G. Seed of *N. Langsdorffii* (× about 50).



ANDERSON AND OWNBEY—SPECIFIC DIFFERENCE

MORPHOGENETIC DIFFERENCES BETWEEN NICOTIANA ALATA AND N. LANGSDORFFII AS INDICATED BY THEIR RESPONSE TO INDOLEACETIC ACID

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Introduction

An unusual opportunity for the application of the present knowledge of hormones to the investigation of morphogenetic differences between two closely related species is afforded by *Nicotiana alata* and *Nicotiana Langsdorffii.* The flowers of the two species are similar, but the difference in the size of the corolla parts suggests a possible interpretation in terms of hereditary response to growth substance. One of the chief differences lies in the constricted part of the corolla-tube (pl. 25, fig. 1). In *N. alata* its length is at least fifteen to twenty times that of *N. Langsdorffii,* whereas the whole corolla in the former is only four or five times the length of the latter. The epidermal cells of the tube of *N. alata* are extremely long; those of *N. Langsdorffii,* relatively short.

The work on several known genetic dwarf races of corn by van Overbeek ('35, '38) indicates that the varietal differences are due to genetic differences which regulate production, use, and inactivation of auxin. The experiments on *Epilobium* hybrids by Schlenker and Mittman, cited by Went and Thimann ('37), suggest this same relationship. If this hypothesis holds true for species of *Nicotiana* and the differences between them are due to differences in amount of hormone produced, then auxin should prove to be a limiting factor in *N. Langsdorffii* and its application to the corollas of this species should then cause an increase in size. If differences are due to differences in ability to use growth substance, then auxin should be a limiting factor in *N. alata* and additional amounts should increase

growth, whereas *N. Langsdorffii* would probably inactivate the hormone. On the supposition that the fundamental morphological distinctions between the two species are linked to genetic differences in ability to use or produce hormone, the following experiments were carried out.

Materials

Nicotiana alata Link & Otto and *Nicotiana Langsdorffii* Wienm. belong to a phylogenetic unit within the genus referred to by Priscilla Avery ('38) as the "alata-group." This is a group appearing to have a center of distribution in the Brazilian and northern Argentine area, and its members possess many morphological and genetic characters in common. The two above species have the same chromosome number and hybridize readily, hybridization occurring at times in nature.

Seeds of both species were planted in the greenhouse October 25, 1938, and flowered from February to April, 1939, inclusive. Flowers and stems were given similar treatment throughout the course of the experiment. One per cent and .5 per cent lanolin pastes were prepared by dissolving the indoleacetic acid (Eastman & Mallinckrodt) in melted lanolin. They were then stored in dark bottles. Due to the instability of indoleacetic acid in water solution the method of Brannon ('37) was followed, the auxin being dissolved in 95 per cent alcohol at a concentration of 4 mg./cc. The water solutions were prepared from this as needed. The alcohol was redistilled to insure purity. Tap water was used in all tests. Water controls were run as checks on solution treatments and pure lanolin controls were used for comparison with the hormone-containing lanolin pastes.

Experimental Methods and Results

Response of Flowers to Indoleacetic Acid

Flowers were studied first as they present the most striking difference between the two species. Four parts of the corolla were recognized; (1) the slender constricted portion of the tube to which the stamens are attached, herein called the tube,

(2) the widened part of the tube, herein called the throat, (3) the gibbous ring of the throat, and (4) the limb (fig. 1). These

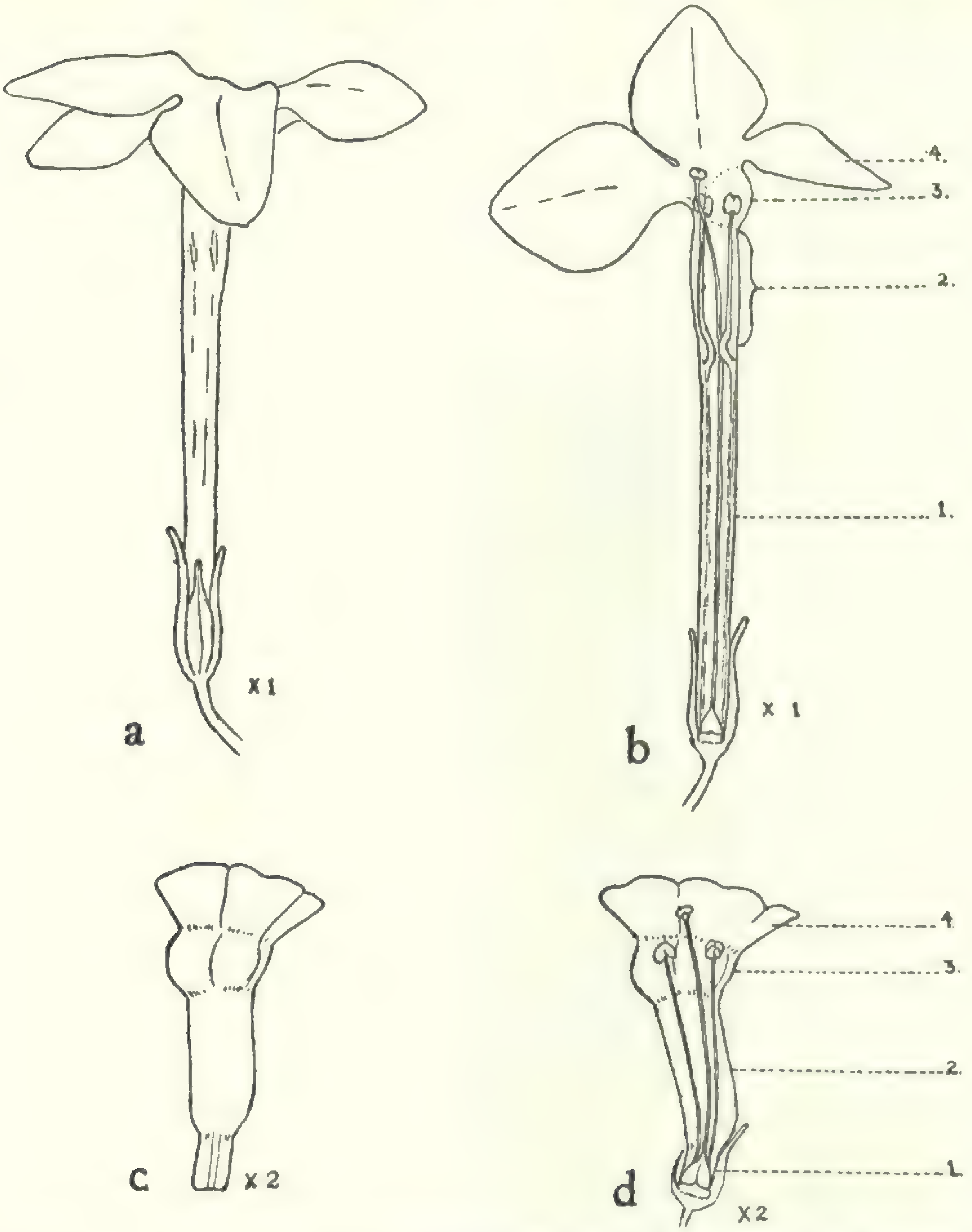

Fig. 1. a and b, external and internal structure of *Nicotiana alata* flowers, c and d, of *N. Langsdorffii*: 1, tube; 2, throat; 3, gibbous ring of throat; 4, limb.

parts show definite differences in cell structure and in growth rate. Direct and indirect methods of supplying additional hormone were used, the direct methods yielding the better results.

Lanolin paste was applied to the tube and throat of both species. In one series of tests one side was smeared with pure lanolin as a control, and the other side with 1 per cent indoleacetic acid-lanolin paste, the two pastes not being permitted to touch. The calyx was cut away in both species to allow the paste to extend to the base of the tube. As a check, untreated flowers of the same size also had the calyx removed. The corollas of *N. alata* ranged from 68 to 75 mm. in length at the time of treatment; those of *N. Langsdorffii,* from 13 to 17 mm. After the corollas were removed from the plant, a narrow strip from each treated side was measured.

As indicated in table I and pl. 25, fig. 2, growth in *N. alata* was stimulated on the side receiving the hormone, a negative curvature of that side resulting within 48 hours. *N. Langsdorffii* showed no perceptible response (table II). If *N. alata* was treated when too mature, no curvature resulted; if too young, the side receiving the hormone became fluted and bulged, but growth in total length was inhibited. The throat showed only slight response or none. Untreated flowers which had only the calyx removed showed no curvature or other alteration. Growth was accelerated regardless of which side of the tube

TABLE I

EFFECT OF APPLICATION OF HORMONE PASTE AND PURE LANOLIN TO OPPOSITE SIDES OF *N. ALATA* COROLLAS

Length of tube		Increment of treated side over untreated	
Side receiving pure lanolin	Side receiving 1% indoleacetic acid-lanolin paste	Length	Percentage
mm.	mm.	mm.	%
46	53	7	15.2
44	50	6	13.6
51	58	7	13.7
47	55	8	17.0
42	49	7	16.6
49	55	6	12.2
48	53	5	10.4
42	48	6	14.3
44	50	6	13.6
33	42	9	27.3
Av. 44.6	51.3	6.7	15.0

received the hormone. Curvature resulted whether or not pure lanolin was applied to the side opposite the one treated with hormone.

TABLE II

COMPARISON OF TUBE LENGTH AFTER TREATMENT OF OPPOSITE SIDES WITH HORMONE PASTE AND PURE LANOLIN*

Species	Length of tube		Increase of treated side
	Side receiving pure lanolin	Side receiving 1% indoleacetic acid-lanolin paste	
	mm.	mm.	%
N. alata	44.9	50.4	12.2
N. Langsdorffii	3.0	3.0	0.0

* Results are the average of 25 flowers each.

In a second series of tests two corollas of the same size were selected and lanolin was applied all around the tube. The controls received pure lanolin, the experimental flowers, 1 per cent indoleacetic acid-lanolin paste. In *N. alata* it was necessary to use two flowers from the same plant, as corolla-tubes maturing on a given parent at any time vary in length only two to five mm., whereas those from different parent stocks vary as much as 20 mm. (table III). The shorter the time elapsing between flower development, the less the variation on a given plant. The last flowers on a branch tended to be definitely smaller. In *N. Langsdorffii* the flowers varied so slightly that they could be taken from any plant. The calyx was again removed. The size of the flower at the time of treatment was the same as in the preceding test. Results with *N. alata* were not as clearly defined as in unilateral treatment but nevertheless indicated the same sensitivity to auxin found in the first test (table IV). Very young flowers of *N. alata* did not give consistent results; those nearly mature did not respond at all. Difficulty arose in finding suitable pairs of flowers of this species. As before, the tube and throat of *N. Langsdorffii* showed no measurable response (table V), except a similar inhibition of growth with both treatments.

TABLE III

VARIATION IN LENGTH OF UNTREATED *N. ALATA* COROLLA-TUBES

Plant no.	Number of tubes measured	Longest	Shortest	Average	Range of variation per plant
		mm.	mm.	mm.	mm.
1	10	55	50	52.1	5
2	7	55	50	52.3	5
3	10	47	45	46.3	2
4	7	54	50	52.5	4
5	10	56	53	54.2	3
6	8	46	42	45.0	4

TABLE IV

LENGTH OF COROLLA-TUBES AND THROATS OF *N. ALATA* TREATED ALL AROUND THE TUBE WITH HORMONE PASTE

Pair no.	Pure lanolin control		1% indoleacetic acid-lanolin paste	
	Tube	Throat	Tube	Throat
	mm.	mm.	mm.	mm.
1	45	25	47	25
2	52	23	55	23
3	51	22	54	24
4	53	23	55	23
5	53	24	54	24
6	48	24	55	24
7	49	27	54	29
8	42	30	47	30
9	32	20	39	24
10	52	23	55	
Average	47.7	24.1	51.5	25.0

TABLE V

LENGTH OF PAIRS OF COROLLA-TUBES FOLLOWING TREATMENT ALL AROUND THE TUBE*

Species	Pure lanolin	1% indoleacetic acid-lanolin paste	Increase
	mm.	mm.	%
N. alata	47.6	51.5	8.2
N. Langsdorffii	3.0	2.9	–3.0

* Results are averages from 25 flowers.

Immature flowers were cut off and floated in a solution of 10 mg. indoleacetic acid per liter of water and measured after 48 hours. A comparable group was floated in water. *N. alata*

corollas of various length were tried, but the only consistent results were that they seemed to mature more slowly than the water controls. In preliminary tests with *N. Langsdorffii* those corollas 17 to 19 mm. in length seemed to show definite increase in limb length and spread, also more blanching than average; a few plants normally showed this tendency. Repetition with two separate groups of fifty corollas each showed this increase in limb length to be consistent (table VI). The corollas had been sorted in pairs of equal size at the beginning of the experiment and one of each pair placed in hormone solution and one in water. If there was any variation in size, the water received the larger flower.

TABLE VI

LENGTHS OF PARTS OF COROLLA OF *N. LANGSDORFFII* FLOATED 50 HOURS IN HORMONE SOLUTION*

Treatment	Limb	Tube and throat	Total length	Limb spread †
	mm.	mm.	mm.	mm.
10 mg. indoleacetic acid/liter	5.0	23.1	28.1	15–17
Control	4.1	22.0	26.1	11–13

* Results are the average of 50 flowers.
† Ten largest only were measured.

Among the various indirect methods of supplying hormone to the flower was the application of lanolin paste to the stem below the inflorescence. When 1 per cent paste was used, there resulted an inhibition of flower buds above the treated area in *N. alata,* a slight inflation of the calyx being followed by yellowing and abscission. The growth of buds on older stems was not immediately checked, but the younger buds were affected. *N. Langsdorffii* showed definite local response such as stem curvature, but this self-fertile species matured seeds as usual above the treated area unless the plants were given extremely heavy doses when very young.

On either side of the stem below the inflorescence strips one-half inch in length were coated with the .5 per cent lanolin paste at three-day intervals. Not a sufficient number of plants of *N. alata* were treated to give conclusive results in a species

as variable as this. However, tube growth seemed to be somewhat accelerated and the average length of the tubes was somewhat greater than in the untreated flowers. Repeated applications often led to an inhibition of growth above the treated area as with the more concentrated paste. The frequent use of pure lanolin caused no change. Two branches of each of several plants were treated, one receiving the hormone, and one pure lanolin. After a time the former ceased to grow but the latter continued development, thus indicating that the hormone was very probably the cause of the inhibition. *N. Langsdorffii* showed no response to the .5 per cent lanolin paste except slight local curvature if application was uneven.

Cut inflorescences of both species were placed in water solution of indoleacetic acid and also in water. To be sure that results were due to the hormone in solution and not to the alcohol which was used to dissolve it, equal amounts of alcohol were added to both. Neither showed any appreciable acceleration of flower size, but a concentration of 10 mg. per liter caused inhibition of floral development in *N. alata*. Solutions of 5 mg. per liter or less resulted in neither bud inhibition nor noticeably larger flowers. The flowers of *N. Langsdorffii* were the same size in the water control and in the auxin solution. While both species keep well when cut, in hormone solution they seemed to keep longer than in water.

In an effort to determine the source of growth substances, styles and stigmas were removed from the flowers of both species while they were still young. In *N. Langsdorffii* it is a simple procedure to open the limb with fine forceps and to reach the style without damaging the corolla and stamens. Except with almost mature specimens of this species the flowers drop off before reaching maturity, usually within 24 to 48 hours after removal of the style. The younger the flowers, the sooner they drop off. The treated flowers were marked with blue on the calyx. Recent experimentation by Bonner and English ('37, '38) has indicated the formation of the wound hormone, traumatin, as a result of tissue damage. This could be a source of error, especially in *N. alata*, as it was impossible to reach the

pistil with available instruments without damaging the corolla and stamens. Therefore, in some of the flowers the limb was cut away with a sharp razor. In half of these the stigma and part of the style were removed; in the other half they were left intact. Even with the limb removed, it was difficult to reach the pistil. The cut inflorescences were then placed in water and covered with a bell jar to reduce transpiration. Previous experience had shown that the flowers on cut inflorescences matured satisfactorily in water. Those flowers with pistils removed tended to develop shorter tubes or to drop off, but some grew normally. On the plants, ten young corollas of various sizes were slit down one side of the tube and the style severed close to the base; others were slit, but the style left intact as controls. Both sets usually matured and the controls were then measured and examined for style injury. Again results were not consistent, but the flowers with severed styles tended toward shorter tubes; the throats were not greatly affected. Curvature toward the injured side developed in both.

Normal cell structure and growth rate of the corolla parts were studied as an aid in understanding the reactions of these parts to indoleacetic acid. Two series of ten corollas of each species were marked off into tube, throat, gibbous ring of throat, and limb by means of fine blue lines. These parts were measured at 24-hour intervals until growth stopped. In *L. Langsdorffii* measurements of growth were started as soon as the corolla parts could be easily distinguished; in *N. alata,* when the corolla was approximately 35–45 mm. in length. Figure 2 represents graphically measurements for the five days preceding full development in *N. alata* and the four days preceding full development in *N. Langsdorffii.*

Cell structure was not studied in detail, but a microscopic examination of the epidermal cells of the various parts was made in order to compare their size and shape. In *N. alata* the epidermal cells of the corolla-tube are extremely long and are similar to those of the *Avena* coleoptile in general shape (fig. 4A), whereas in *N. Langsdorffii* they are comparatively short, almost isodiametric (fig. 4B). As the growth rate of the

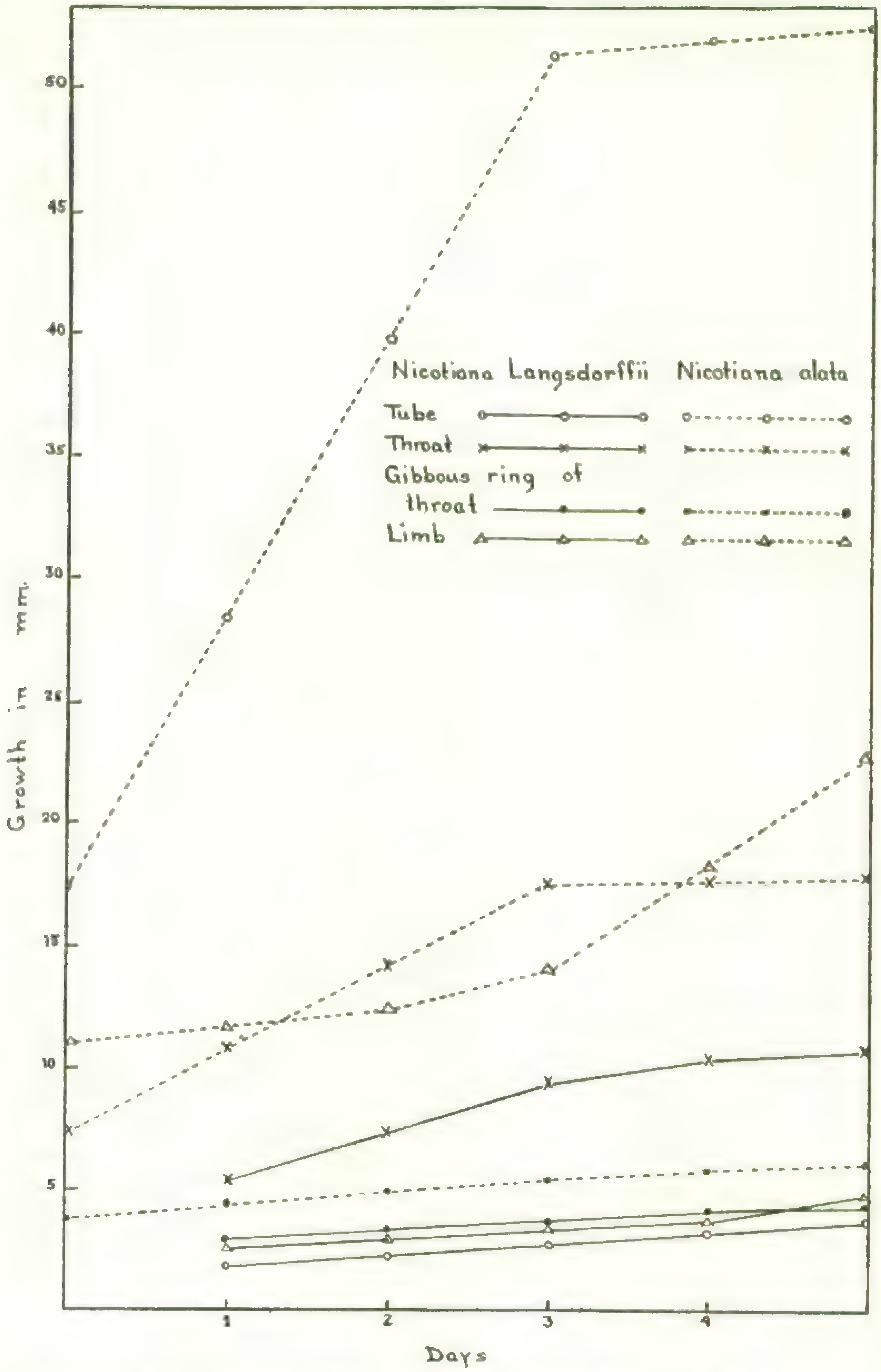

Fig. 2. Growth rates of corolla parts of *Nicotiana alata* and *N. Langsdorffii*. Results are the means of 15 corollas.

tube of *N. alata* is very rapid and that of *N. Langsdorffii* very slow (fig. 3), a correlation between growth rate and cell elongation is indicated. The cells of the throats of the two species are

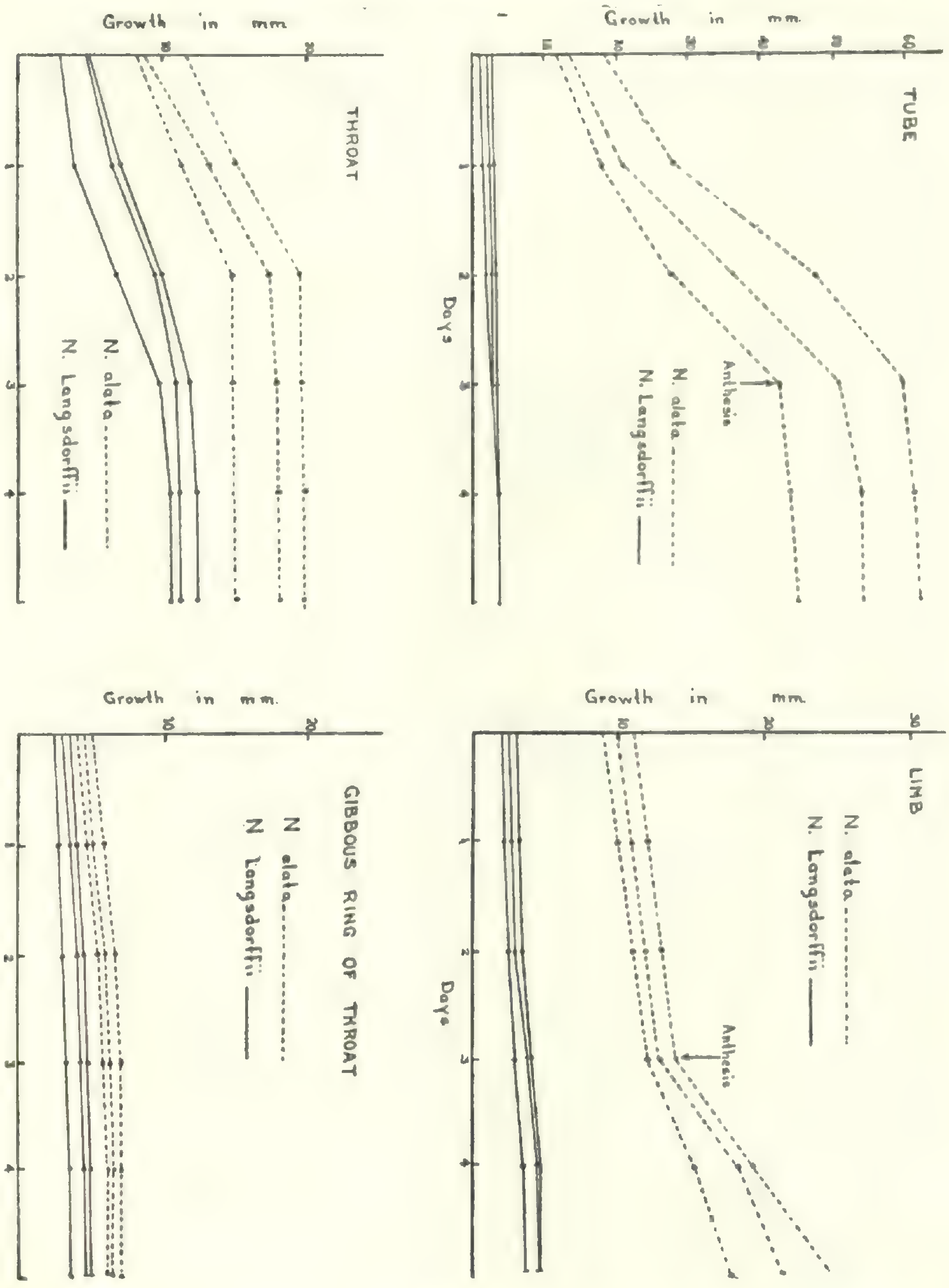

Fig. 3. Growth rates of corolla parts of *Nicotiana alata* and *N. Langsdorffii*. Three typical flowers used for each.

similar in size and shape (fig. 4E, F) and growth rate (fig. 3). They are shorter than those of the *N. alata* tube. In both species the cells of the gibbous ring of the throat show a grad-

ual transition from the longer ones of the throat to the isodiametric cells of the limb (fig. 4C). The two species also have similar growth curves (fig. 3). Many stomata are present.

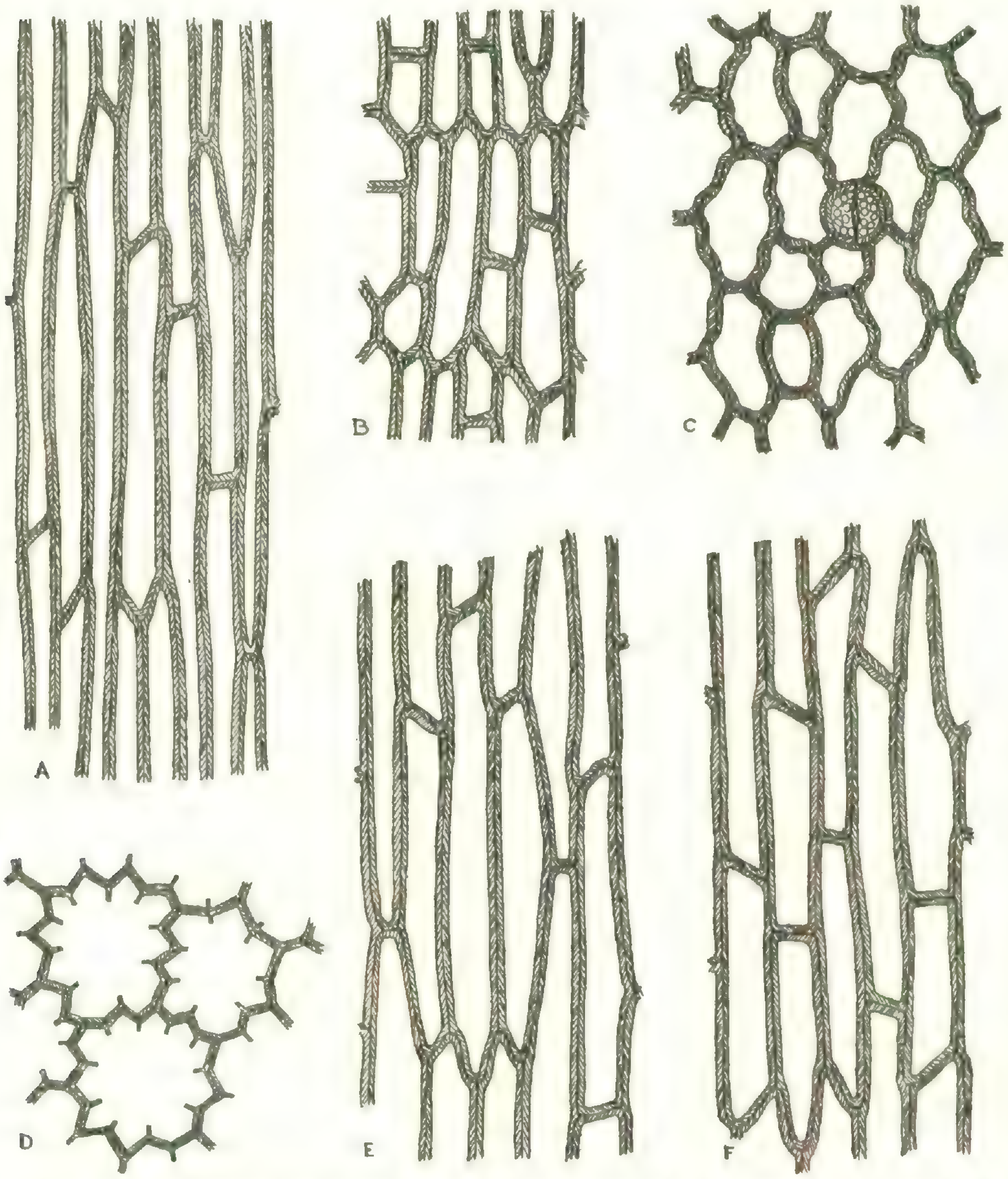

Fig. 4. Epidermal cells of the corolla parts of *Nicotiana alata* and *N. Langsdorffii:* A, tube of *N. alata;* B, tube of *N. Langsdorffii;* C, gibbous ring of throat of *N. alata* (these cells show a gradual transition from throat to limb); D, limb of *N. alata;* C and D are similar in *N. Langsdorffii;* E, throat of *N. alata;* F, throat of *N. Langsdorffii.*

While cells of the limb correspond very closely in the two species (fig. 4D), those of *N. alata* grow more rapidly, especially during the last few days of development (figs. 2–3). It is interesting that in *N. alata* the growth curve of the limb rises at

about the time of anthesis as the tube and throat curves flatten out.

STEM RESPONSE TO INDOLEACETIC ACID

A peculiar curvature of the stem in *N. alata,* apparently resulting from the action of the hormone, suggested a limited study with stems of both species. Young flower stalks were used; old ones in which growth had practically stopped did not respond. If the primary stalk was used, it was cut off 45 to 60 cm. from the tip; secondary ones were of necessity much shorter. These were placed in solutions of (a) 10 mg. of indoleacetic acid/liter, (b) 5 mg./liter, (c) 1 mg./liter, and (d) tap water. Solutions were changed every other day until three or four treatments were given. Then the stems were placed in water which was changed as needed.

With a concentration of 10 mg./liter, *N. alata* showed increased growth on the side opposite the insertion of the leaf in the younger parts of the stem and therefore marked curvature of the stem in the region of the upper leaves (fig. 5). This occurred in from two to five days from the beginning of treatment, the younger stems responding more quickly. At this concentration the flower buds which were nearly mature continued normal development, while the younger buds turned yellow and abscissed (pl. 26, fig. 2). With a concentration of 5 mg./liter, the stem curvature was slight and the flowers matured in the same time as those of the controls (pl. 26, fig. 1). No effect was apparent with weaker solutions, nor with the small amount of alcohol used to dissolve the hormone, 2½ cc. per liter.

While *N. Langsdorffii* also showed curvature with a concentration of 10 mg./liter, it was much less pronounced (pl. 26, fig. 2). The flower buds were not affected.

Roots developed freely from the stem surface of *N. alata* in the region where indoleacetic acid solution had been applied. Both 5-mg. and 10-mg./liter solutions stimulated abundant root production. Stems also developed roots without treatment, but only near to the base, and they were not as numerous as on the treated stems. These results are in agreement with

Fig. 5. *Nicotiana alata*, showing curvature when stem was placed in a solution of 10 mg. indoleacetic acid/liter. Note that curvature is convex opposite insertion of leaf.

those of Stuart ('37) and Pearse ('38), who have found root development accelerated by auxin. According to Brase ('37), failure to produce roots was not overcome in many species by use of synthetic growth substances. This seemed to be true of *N. Langsdorffii,* which did not produce roots either with or without treatment.

As previously mentioned, applications of 1 per cent indoleacetic acid-lanolin paste will induce local curvature of the stems in the treated region in both species. Even with one treatment, roots will finally break through the epidermis in *N. alata.* Inhibition of floral development above the treated area was complete, although branches below matured normally (pl. 26, fig. 3). *N. Langsdorffii* showed no inhibition and no root formation, but matured its flowers and seeds normally in spite of extreme curvature (pl. 26, fig. 4). Growth was checked in this species only when high concentrations were used daily on young stems. External roots did not appear. A concentration of 0.5 per cent indoleacetic acid in lanolin produced the same type of result as the more concentrated paste, but to a less degree. *N. alata* showed gradual inhibition of growth above the treated area; very few roots developed.

Discussion

The response of a plant to additional growth substance is conditioned by its sensitivity and its tendency to inactivate auxin. The curvature of the corolla-tube in *N. alata* following application of indoleacetic acid-lanolin paste indicates that this species has the ability to use additional hormone. This was also suggested by the increase in length of corolla-tubes following application of hormone paste all around the tube. Like the cells of the *Avena* coleoptile, the tube cells of *N. alata* respond readily to growth substance. Microscopic examination indicates that this increased growth in *N. alata* is the result of increased cell elongation rather than division. Cells of this type which in nature elongate rapidly are thought to be often capable of using auxin for further elongation. The short tube cells of *N. Langsdorffii* show no response to hormone with any

method used. This indicates a probable inherent lack of ability to utilize growth substance, possibly due to lack of sensitivity to it or to its inactivation by oxidative destruction or enzyme activity. The difference in the tubes of the two species, not only in size but in cell structure and growth rate also, is probably due to the heritable genetic difference in the ability of their cells to respond to growth substance.

The throats of the two species are similar in cell size and growth rate. In neither species did the throat show marked response to addition of growth substance. The limb of *N. alata* grew more rapidly than *N. Langsdorffii* during the last few days of development. The development of the corollas floated in hormone solution possibly gives some insight into the effect of the hormone. Isolated corollas of *N. alata,* in which growth is normally very rapid, showed no increased growth over controls, but both were considerably shorter than normal. Recent work of Alexander ('38) and Stuart ('38) has indicated that one of the effects of hormones such as indoleacetic acid in stimulating growth is the mustering of the food factor. *N. alata* normally grows with such rapidity that the food present in isolated corollas is probably soon exhausted and further growth then limited. *N. Langsdorffii,* which is comparatively unresponsive to indoleacetic acid in other parts of the corolla, shows increased growth of the limb when floated in hormone solution. This tendency was noted also after the application of lanolin paste, although exact measurements were not made. If auxin is considered to be one of the factors necessary for growth, it may be that not enough reaches the limb to allow optimum development and thus it becomes a limiting factor. Perhaps this explains why with direct application these cells are stimulated to increased growth.

Since it is generally the terminal bud which produces hormone, the stigma and style, being considered the possible counterpart of the terminal bud, were removed to study the effect on the flower. That *N. Langsdorffii* flowers wilt and drop off after removal of these parts, unless nearly mature at the time, was considered as evidence that they may control the de-

velopment of the flower in some way. Went and Thimann ('37) make the general statement that auxin is one of the many factors necessary for the ordinary growth process and that "without auxin, no growth." Absence of auxin may thus account for the lack of development. However, Avery and LaRue ('38) have found that decapitated *Avena* coleoptiles will continue development on agar culture containing food and minerals for as much as six days after all measurable traces of growth substance have been used up. The hormone is therefore probably not a necessity for growth although it does stimulate or "catalyze" it. On the other hand, *N. alata* flowers are often developed after the removal of the stigma and part of the style, although with shorter tubes than usual. Growth is limited, but not often stopped. This may be due to inhibition caused by the wound hormone, traumatin, or it may be that some other source supplies the growth substance. It is also possible that all of the long style was not removed and that there is a "regeneration of a physiological tip"; or that the part of the style remaining still produces enough auxin for limited growth.

A study of the flowers of the two species seems to indicate that their differences lie in genetic differences in response to hormone, *N. alata* being sensitive to it, *N. Langsdorffii* lacking in ability to use it or inactivating it.

When cut young flower stalks were placed in hormone solution, the "unphysiologically" high concentration of indoleacetic acid—10 mg./liter—was carried upward in the transpiration stream (Hitchcock and Zimmerman, '35). This is not in opposition to the usual concept of polarity expressed by Went and Thimann ('37). The curvature of the young stems was brought about by greater growth on the side opposite the leaves. The lessened growth in the region of the leaf insertion may have been caused by a lower concentration of hormone in the stem owing to its passage into the leaf. Old stems show no curvature because the aging of the cells renders them unresponsive. *N. alata,* with characteristic sensitivity and good transport facilities, curved strongly, the degree of curvature depending upon age of the cells and concentration of the hor-

mone. In the cut stems of *N. Langsdorffii* the hormone was probably likewise carried upward in the transpiration stream, but the resulting slight curvature showed little use of the additional hormone. It is possibly significant that the total height of *N. alata* is greater, 150 to 190 cm., than of *N. Langsdorffii,* 110 to 120 cm. Both species respond to local application of 1 per cent indoleacetic acid-lanolin paste in young stem regions. As this is also an "unphysiologically" high concentration of hormone, unequal application of it stimulates *N. Langsdorffii* locally to marked curvature but no roots appear. Due to the destruction of the hormone in transport or to lack of sensitivity of this plant to it, the flowers and other parts were not affected. *N. alata* showed similar local curvature of the stem with formation of adventitious roots.

The effects from both lanolin application and solution treatment are not limited to the stems of *N. alata,* but are extended to the flower stalk. With the concentrations used, growth was completely inhibited and flower buds and upper nodes of the flower stalk were eventually killed. This again seems to indicate that inactivation does not occur in *N. alata,* as a high concentration of the substance apparently reaches the flowers.

Because of the great sensitivity of the cells of *N. alata* to hormone, the concentrations used proved to be toxic to the younger cells. That very young corollas do not respond favorably to applications of lanolin paste might be explained by this fact. The upper tissue is perhaps partly inactivated by the mobilization of food materials in the treated area of *N. alata* as this region responds with the formation of numerous roots; and development of roots requires food material. The differentiation of the tissue to form roots on the stem would possibly interfere mechanically with transport and aid in causing inhibition above the region of application. Cut flower stalks of *N. alata* produced some basal roots without any treatment, but more if treated with 5 or 10 mg. indoleacetic acid/liter. *N. Langsdorffii,* however, produces none under such conditions, thus giving additional evidence that *N. alata* probably is hereditably more able to use growth substance. As is

usually true, *N. alata* roots more quickly when treated. It has been suggested by Went ('38, '39) and Cooper ('38) that indoleacetic acid stimulates rooting by causing a redistribution and then an activation of the rhizocaulin already present in the tissue.

Went and Thimann ('37), in the light of the work of Lehman, Hinderer, Schlenker, and others, on *Epilobium* hybrids, suggest that possibly the sensitivity to growth hormone might be determined by the genes; the auxin production, by the cytoplasm. The above results suggest that morphogenetic differences in hormone response probably account for the principal differences between the two species studied.

Summary

1. The corollas and flower stalks of *Nicotiana alata* and *Langsdorffii* were used in studying the role of growth hormones in morphogenesis.

2. The corollas were found to serve as especially favorable material since they follow the same general growth pattern, but differ markedly in cell elongation. Results indicate that *N. alata* generally has greater ability to use additional hormone than *N. Langsdorffii.* The former also is more sensitive and smaller amounts prove toxic to young cells. Corollas of *N. Langsdorffii* give evidence of inactivation of growth hormone except in the limb.

3. Young flower stalks inserted in hormone solution respond by curvature on the side opposite the leaf insertion. The response is much greater in *N. alata* than in *N. Langsdorffii,* and in both species depends upon the age of the stem and the concentration of the hormone.

4. Experiments indicate that many of the principal differences between the two species lie in a genetically controlled difference in their ability to use hormone.

I wish to take this opportunity to express my appreciation to Dr. Edgar Anderson, of the Henry Shaw School of Botany, for suggesting the problem and for the use of the greenhouse and materials; to Dr. George T. Moore, Director of the Mis-

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EXPLANATION OF PLATE

PLATE 25

Fig. 1. At left, inflorescence of *Nicotiana alata;* at right, inflorescence of *Nicotiana Langsdorffii.*

Fig. 2. Curvature of *Nicotiana alata* in response to treatment with 1 per cent indoleacetic acid-lanolin paste. In flower at left, right side of tube had been treated with hormone paste; left side with pure lanolin. Flower at right was untreated.

1

2

NAGEL—NICOTIANA ALATA AND N. LANGSDORFFII

Explanation of Plate

PLATE 26

Fig. 1. Stems of *Nicotiana alata* which were placed in a solution of indoleacetic acid. A was treated with a solution of 5 mg./liter; B, with a solution 10 mg./liter. Note greater curvature and bud inhibition in the latter.

Fig. 2. Stems of *Nicotiana* kept in a solution of 10 mg. indoleacetic acid/liter for four days. Left, *N. Langsdorffii;* right, *N. alata.* Note greater bud inhibition and stem curvature in *N. alata.*

Fig. 3. *Nicotiana alata* stem treated with 1 per cent indoleacetic acid-lanolin paste. Note the inhibition of growth and abscission of buds above the treated area. The white spots in the treated area are roots.

Fig. 4. *Nicotiana Langsdorffii* stem showing curvature which followed treatment with 1 per cent indoleacetic acid-lanolin paste. Floral development is not checked and seeds mature as usual above the treated area.

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4

NAGEL—NICOTIANA ALATA AND L. LANGSDORFFII

MONOGRAPH OF THE NORTH AMERICAN SPECIES OF THE GENUS EPHEDRA[1]

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Introduction

The importance of the drug, ephedrine, secured from Asiatic species of *Ephedra,* in the treatment of nasal colds, asthma and hay fever has attracted wide attention to this genus. Workers in range management have investigated the relative palatability of various species, and students of phylogeny have speculated on the role of the genus in a phylogenetic sequence. These last have contributed to the confusion in the terminology for, in addition to applying descriptive terms derived from Angiosperm and Gymnosperm sources, they coined new ones. Unfortunately, many of the investigations are of little value because the material was incorrectly identified or was a mixture of more than one species.

Correct determination of material is extremely difficult, for the number of species has nearly doubled since the publication of the last monograph of the entire genus and many of them were originally described from sterile or from staminate material. Approximately two-thirds of collected specimens cannot be identified with certainty from existing descriptions. The present study determines the correct application of names, proposes several new ones for hitherto undescribed forms, delimits the North American species, and provides means for their accurate determination. The South American species are not discussed in the present work but will be taken up later.

Manuals, floras, and other works which recognize species of

[1] An investigation carried out at the Missouri Botanical Garden in the Graduate Laboratory of the Henry Shaw School of Botany of Washington University and submitted as a thesis in partial fulfillment of the requirements for the degree of doctor of philosophy in the Henry Shaw School of Botany of Washington University.

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Ephedra are not cited in the text of this paper unless they are necessary for bibliographical reasons. Such citations might indicate acceptance of the entities as delimited in those works, which is usually not the case. The more important publications may be found in the history, generic and specific synonymy, and bibliography.

HISTORY

Ephedra has been known and used medicinally in China for about five centuries. Its general acceptance by Western pharmacists is comparatively recent. Groff and Clark[2] summarize the history of its use in medicine and indicate the scant value many analyses have because the material upon which they are based is not definitely determined. To be serviceable, analyses of the plants should be accompanied by the name of the species and the location of herbarium material, the locality in which it grew, the date of collection, the parts of the plant analyzed, and the methods of drying, of extraction and of measurement.

The genus *Ephedra* was definitely established by Linnaeus in the 'Species Plantarum'[3] and in the 'Genera Plantarum'[4] of 1753 and 1754 respectively. Two species, *E. distachya* and *E. monostachya,* were included by him in the former publication. The first North American species to be described was *E. antisyphilitica* in C. A. Meyer's[5] monograph of the entire genus. In 1848 Torrey[6] recorded another species as "*Ephedra occidentalis*" which was later validly published by Watson[7] as *E. trifurca.* Watson[8] described three species, *E. californica, E. nevadensis,* and *E. Torreyana,* in 1879; and four years later[9] published *E. aspera* and *E. pedunculata* from the notes of Engelmann. The second and latest monograph of the genus

[2] Groff & Clark in Univ. Calif. Pub. Bot. **14**: 247–282, *charts 1–6.* 1928.

[3] L., Sp. Pl. **2**: 1040. 1753.

[4] L., Gen. Pl., ed. 5, 462. 1754.

[5] Meyer, C. A. in Mém. Acad. Imp. Sci. St. Petersburg. VI, Sci. Nat. **5**: 291. 1846.

[6] Torr. in Emory, Mil. Reconn. 151. 1848.

[7] Wats. in U. S. Geol. Surv. Fortieth Parallel [Bot. King's Exp.] **5**: 329. 1871.

[8] Wats. in Proc. Am. Acad. **14**: 299. 1879.

[9] Wats. in Proc. Am. Acad. **18**: 157. 1883.

appeared in 1889, and in it Stapf[10] published two subvarieties of *E. nevadensis,* subvar. *paucibracteata* which is synonymous with the species, and subvar. *pluribracteata* which is a synonym of *E. viridis* Coville[11] published in 1893. In 1909 the most southern of the North American species, *E. compacta,* was described by Rose.[12] Johnston[13] in 1922, and Cory[14] in 1938, described *E. peninsularis* and *E. Reedii* respectively, both of which are synonyms for *E. aspera.* Groff and Clark[15] published a survey of the North American species in 1928 as an aid to the study of the drugs contained in plants of the genus. Nelson[16] described *E. fasciculata* from vegetative material in 1935, and in the same year Coville and Morton[17] proposed *E. funerea,* and Reed[18] *E. texana,* which is synonymous with *E. antisyphilitica. E. Coryi* Reed[19] was published in 1936, and in 1938 *E. Reedii* Cory and *E. antisyphilitica* var. *brachycarpa* Cory[20] appeared.

General Morphology

The North American members of the genus are, with the exception of the clambering *E. pedunculata,* erect woody shrubs. All species have reduced scale-like leaves and photosynthetic young stems.

Seedlings.—The tap-root of the young seedlings soon branches to form a fibrous root system with numerous root hairs and a diarch or occasionally triarch stele. Two cotyledons are produced. The first leaves of all species are borne in pairs, and the ternately leaved forms show the whorled arrangement only after several pairs have been produced. In *E.*

[10] Stapf in Denkschr. K. Akad. Wiss. Wien **56**[2]: 1–112, *pls. 1–6, 1 map.* 1889.
[11] Coville in Contrib. U. S. Nat. Herb. **4**: 220. 1893.
[12] Rose in Contrib. U. S. Nat. Herb. **12**: 261. 1909.
[13] Johnston in Univ. Calif. Pub. Bot. **7**: 437. 1922.
[14] Cory in Rhodora **40**: 216. 1938.
[15] Groff & Clark in Univ. Calif. Pub. Bot. **14**: 247–282, *charts 1–6.* 1928.
[16] Nelson in Am. Jour. Bot. **21**: 573. 1935.
[17] Coville & Morton in Jour. Wash. Acad. Sci. **25**: 307. 1935.
[18] Reed in Bull. Torr. Bot. Club **62**: 43. 1935.
[19] Reed in Bull. Torr. Bot. Club **63**: 351, *figs. 1–2.* 1936.
[20] Cory in Rhodora **40**: 218. 1938.

Torreyana the endosperm remains attached to the base of the stem by means of a foot, although Voth[21] indicates that *Ephedra* is the only Gnetalean genus lacking this organ.

From 420 seeds of *E. trifurca, E. Torreyana, E. antisyphilitica, E. aspera, E. Coryi* var. *viscida* and *E. viridis,* in about equal numbers gathered in May and June and planted in September, only eleven seedlings were obtained, nine of *E. Torreyana* and one each of *E. trifurca* and *E. Coryi* var. *viscida.*

No seedlings and only a very few young plants were observed during two seasons of field work, and it is probable that the most frequent type of propagation is by means of divisions of buried stems. It has been suggested that the peridermal diaphragm at the base of each internode which allows the stems to fragment readily is a device to aid propagation by the rooting of the segments. It is highly improbable that many of these segments would root under the xerophytic conditions characteristic of the habitat of *Ephedra.*

Stem.—The green stem is solid, furrowed, and usually roughened by the cutinized and thickened epidermal walls which contain calcium oxalate. Blunt papillae occur on the thickened walls, and the size and number of these determine the degree of asperity of the stem. While the papillae vary greatly within a species, the width of the furrows and ridges and the number of stomata per unit of area remain nearly constant. The epidermal cells upon the ridges are longer than those in the furrows and are underlain by a bundle of hypodermal fibers.

In most species the stomata are confined to the furrows and usually are sunken, although in *E. antisyphilitica, E. compacta* and *E. pedunculata* the striation is not extensive and the stomata are scattered over the entire surface. The stomatal pits are prominent in these three species, especially in *E. compacta.* The size and shape of the stomata vary with the species.

Stomatal frequencies are relatively constant for each species, provided stems of the same age and from plants in almost similar habitats are examined. While it would be bet-

[21] Voth in Bot. Gaz. **96**: 298. 1934.

ter to use the stomatal index ($I = \frac{s}{e-s} \times 100$, where *s* is the frequency of stomata and *e* the frequency of epidermal cells in the same unit area) selection of the material to be examined makes it possible to secure figures subject to only slightly greater variation. The cells on the edges of the ridges are difficult to see without special preparation, but Pont[22] in studies on two species of plants did not count the epidermal cells upon the ridges. Frequently, however, it is difficult to distinguish between the cells of the furrows and those of the edges of the ridges, although the latter are usually longer.

By utilizing supplementary characters such as those just mentioned it is possible to identify almost any specimen of *Ephedra* from North America. Table I lists figures which will aid in the determination of vegetative as well as staminate and ovulate material.

The outer layers of cortical cells are chlorophyll-bearing and include numerous air spaces. Starch grains, calcium oxalate crystals and tannin are enclosed within many of these cells. Three systems of fibers are distinguished in this region by Graham[23]: the hypodermal, which underlies the ridges, as hitherto mentioned; the mesocortical, which is scattered through the cortex; and the pericyclic, which is scattered about on the periphery of the stele with the largest fibers abutting the vascular strands. The hypodermal fibers and those of the pericycle which adjoin the vascular bundles are the most constant in numbers and in size. At the nodes this fiber system is interrupted.

Lignified cells and fibers are found in the pith, and a peridermal diaphragm is produced at the base of each internode, which, with the interruption of the fiber system, allows ready fragmentation of the stems.

The stele is an endarch siphonostele with a slight variation in the numbers of bundles. Those species characterized by ternate arrangement of the leaves and bracts have three pairs

[22] Pont in Beih. z. Bot. Centr. **59**: 214–224, *6 figs.* 1939.

[23] Graham in Trans. Roy. Soc. Edinb. **46**: 203–212, *3 pls.* 1909.

TABLE I

COMPARISON OF NORTH AMERICAN EPHEDRAS

	Average length of internode in cm.	Number of leaves or bracts in a whorl	Average angle of branch divergence in degrees	Number of vascular bundles in a stem	Number of hypodermal fiber strands	Number of cells in a cross-section of a fiber strand	Number of stomata per sq. mm.	Ovulate bracts: membranaceous, herbaceous or fleshy	Number of seeds in strobilus	Peduncle of ovulate strobilus: present or absent	Usual number of anthers on antherophore
1. *E. trifurca*	3.6	3	30	12–15	40	28	108	mem.	1–3	ab.	5
2. × *E. intermixta*	2.6	3	35–40	15	36	11	120	mem.	1–3	ab.	4–7
3. *E. Torreyana*	2.4	3	48	12–15	48	4	88	mem.	1–3	ab.	7
4. × *E. arenicola*	3.5	2–3	35	10–12	34	14	50	mem.	1–3	pr.	6
5. *E. funerea*	4.	3	60	12–15	60	5	84	mem.	1–3	ab.	7
6. *E. californica*	3.8	3	45	12–15	36	9	92	mem.	1	ab.	7
7. *E. aspera*	3.	2	35	10	40	10	68	mem.	1	ab.	5
8. *E. fasciculata*	2.5	2	35	10	48	4	72	mem.	1	ab.	6
9. *E. Clokeyi*	3.	2	40	10	50	7	48	mem.	1	ab.	6
10. *E. nevadensis*	2.8	2	45	10	56	7	84	herb.	2	pr.	8
10a. *E. nevadensis* f. *rosea*	2.8	2	42	10	40	9	60	herb.	2	pr.	–
11. *E. viridis*	2.5	2	33	8–10	39	7	52	mem.	2	pr.	7
12. *E. Coryi*	2.5	2	22	8–10	34	12	48	flsh.	2	pr.	7
12a. *E. Coryi* var. *viscida*	3.6	2	28	10	35	16	52	herb.	2	pr.	6
13. *E. antisyphilitica*	2.8	2	48	10	20	5	76	flsh.	1	ab.	6
13a. *E. antisyphilitica* var. *brachycarpa*		2							1		
14. *E. compacta*	2.	2	37	10	12	14	96	flsh.	2	ab.	–
15. *E. pedunculata*	4.	2	52	8–10	18	12	56	flsh.	2	pr.	6

or three groups of three small bundles. In forms with binate arrangement of parts the vascular system consists of two pairs of large bundles alternating with two pairs or with three groups of three small bundles.

The xylem consists of spiral primary elements and secondary tracheids and vessels with bordered pits. These last are modified tracheids, and the oblique end walls have bordered pits larger than those on the lateral walls. These pits enlarge to lose both torus and border and occasionally fuse.[24]

The primary phloem consists of cambiform parenchyma elements and narrow sieve-tubes with oblique plates.

The wood rays are large, uniseriate in young wood, multiseriate in older branches, and consist of storage parenchyma and transformed longitudinal fibers. The pits are small and simple. Depressions in the wood correspond to the positions of the large rays. There is no apparent relation between the position of the rays and that of the leaf traces.

The angle formed by the branches with the stem in any species is relatively constant, although the amount of branching and the length of branches and of internodes are variable within limits for each species and are altered by changes in environmental conditions.

Leaves.—The leaves are small, scale-like, and usually connate. The median and basal portions are thickened, and an abscission layer developed near the base renders the leaf caducous in most species. The leaves are either opposite or ternate and the whorls alternate.

Strobili.—All the North American species are essentially dioecious, but it is often possible to find a plant of any species which bears strobili of both types. I have also seen bisporangiate strobili on otherwise staminate plants of *E. trifurca, E. Torreyana, E. aspera* and *E. Clokeyi.* Bisporangiate strobili were not found on ovulate plants. Apparent sexual differentiation is confined to the peduncles and strobili.

The staminate strobili are compound and borne in pairs or

[24] Jeffrey, The anatomy of woody plants, p. 367. 1917.

whorls at the nodes of the young branches, or rarely terminally. They consist of an axis bearing 2–13 whorls of binately or ternately arranged bracts, all except the lower subtending a vasiform perianth which surrounds a staminal column. Upon this column, or sporangiophore, are borne the three to twelve usually bilocular anthers which may be sessile or stipitate. The column in some species is very variable. In *E. Clokeyi* it may attain a length three times the normal, and in *E. Torreyana* a slender column may bear one uniloculate anther or a branched column may bear up to ten bi- and triloculate anthers. The bract and perianth are more constant in size within the species, and outlines of these and typical columns are figured in plate 27.

The ovulate strobili are solitary or whorled at the nodes of the young branches and may be sessile or long-pedunculate. Three to twenty whorls of membranaceous to fleshy bracts surround the one to four ovules. The ovule is enclosed by two integuments, the inner extending through an opening of the outer to form a tubillus which leads to the pollen chamber at the tip of the ovule. Although the form of the tubillus was used as a character in the delimitation of species by both Meyer and Stapf, it varies somewhat in most of the American species and is not of great value as a diagnostic character. The length of the peduncle, the number, shape, size and texture of the bracts, and the character and numbers of seeds (pl. 27) are the most valuable characters in delimitation of species.

Phylogeny and Geographical Distribution

It is possible to trace a probable course of evolutionary development among the American species of *Ephedra,* but such speculation is of little value unless based upon a thorough knowledge of the entire genus. The apparent differences between species of even separate continents are often so slight that all must be considered in any theorizing upon developmental sequences. The key to the species is artificial, and the entities are grouped only so that the most similar ones are close together.

The distribution maps (pl. 28) are fairly accurate with the exception of Nevada and Mexico, where an insufficient number of collections have been made. The region of greatest specific concentration for North America is in west-central Arizona where seven of the eighteen entities occur.

Acknowledgments

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Entire or partial collections of *Ephedra* were borrowed from several institutional and private herbaria, and certain herbaria were visited. To these institutions and individuals the author wishes to express his gratitude. These herbaria are indicated in the text by the following abbreviations:

(BYU) —Brigham Young University.

(Buf) —Buffalo Museum of Science.

(CA) —California Academy of Sciences.

(Clo) —Herbarium of I. W. Clokey.

(F) —Field Museum of Natural History.

(G) —Gray Herbarium of Harvard University.

(I) —Iowa State College.

(M) —Missouri Botanical Garden.

(NMAM)—New Mexico State College of Agriculture and Mechanic Arts.

(P) —Pomona College.

(R) —Rocky Mountain Herbarium of the University of Wyoming.

(S) —Leland Stanford University.

(SD) —San Diego Natural History Museum.

(T) —Agricultural and Mechanical College of Texas.

(TTC) —Texas Technological College.
(UC) —University of California.
(UI) —University of Iowa.
(UNM) —University of New Mexico.
(UW) —University of Wisconsin.
(US) —United States National Herbarium.

TAXONOMY

Ephedra [Tourn.] L., Sp. Pl. **2**: 1040. 1753; Gen. Pl., ed. 5, 462. 1754; C. A. Meyer in Mem. Acad. Imp. Sci. St. Petersburg, VI, Sci. Nat. **5**: 291. 1846; Endlicher, Syn. Conif. 253. 1847; Torr. in Emory, Mil. Reconn. 151. 1848; Torr. in Emory, Rep. U. S. & Mex. Bound. Surv. **2**: 207. 1859; Parl. in DC., Prodr. **16**^{2}: 352. 1868; Wats. in U. S. Geol. Surv. Fortieth Parallel [Bot. King's Exp.] **5**: 328. 1871; Parry in Am. Nat. **9**: 351. 1875; Wats. in Proc. Am. Acad. **14**: 298. 1879; Wats., Bot. Geol. Surv. Calif. **2**: 108. 1880; Wats. in Proc. Am. Acad. **18**: 157. 1883; Stapf in Denkschr. K. Akad. Wiss. Wien **56**^{2}: 1. 1889; Coult. in Contrib. U. S. Nat. Herb. **2**: 552. 1894; Rydb. in Colo. Agr. Exp. Sta. Bull. [Fl. Colo.] 100: 10. 1906; Rose in Contrib. U. S. Nat. Herb. **12**: 261. 1909; Coult. & Nels., Man. Rky. Mt. Bot. 19. 1909; Jepson, Fl. Calif. 65. 1912; Wooton & Standl. in Contrib. U. S. Nat. Herb. **19**: 38. 1915; Goldman in Contrib. U. S. Nat. Herb. **16**: 315. 1916; Rydb., Fl. Rky. Mts. and Adj. Plains, ed. 1, 19. 1918, ed. 2, 19. 1923; Standl. in Contrib. U. S. Nat. Herb. **23**: 63. 1920; Johnston in Univ. Calif. Pub. Bot. **7**: 437. 1922; Abrams, Ill. Fl. Pac. States, 77. 1923; Davidson & Moxley, Fl. So. Calif. 31. 1923; Jepson, Man. Fl. Pl. Calif. 61. 1925; Tidest. in Contrib. U. S. Nat. Herb. **25**: 56. 1925; Rehder, Man. Cult. Trees & Shrubs, 67. 1927; Groff & Clark in Univ. Calif. Pub. Bot. **14**: 247. 1928; George, Supp. aux Mém. Soc. Sci. Nancy **1930**: 29. 1930; Coville & Morton in Jour. Wash. Acad. Sci. **25**: 307. 1935; Jepson, Man. So. Calif. Bot. 19. 1935; Nelson in Am. Jour. Bot. **21**: 573. 1935; Reed in Bull. Torr. Bot. Club **62**: 43. 1935; Reed in Bull. Torr. Bot. Club **63**: 351. 1936; Cory in Rhodora **40**: 216. 1938.

Chaetocladus Senilis [=Nelson] Pinac. 161. 1866.

Erect or clambering, dioecious or rarely monoecious shrubs; branches equisetoid, solitary, or whorled; vascular cylinder an endarch siphonostele; wood rays large, uniseriate in young wood, multiseriate in older branches, composed of storage parenchyma and transformed longitudinal wood fibers; wood containing vessels with oblique terminal walls perforated by numerous pits larger than those on lateral walls, the membranes of these terminal pits lost at an early stage, the pits occasionally fused to form slits; leaves binate or ternate, small, usually united to form a sheath; staminate strobili compound, binately or ternately whorled bracts including a vasiform structure composed of the base of the antherophore upon which are borne the few to many usually biloculate sessile to short-stipitate anthers; ovulate strobili with few to many whorls of binately or ternately arranged membranaceous to fleshy bracts surrounding the one to several ovules, the inner integument extended to form a cylindrical projecting tubillus; two archegonia usually present.

Type species: *Ephedra distachya* L., Sp. Pl. **2**: 1040. 1753.

ARTIFICIAL KEY

A. Leaves and bracts of spikes ternate.
  B. Leaves becoming shredded and gray with age, persistent; terminal buds spinose.
    C. Leaves more than 8 mm. long .... *1. E. trifurca*
    CC. Leaves less than 8 mm. long .... *2. E. intermixta*
  BB. Leaves remaining firm or falling off with age; terminal buds not spinose.
    D. Seeds less than one-half as wide as long, cream to light brown, rough and angular.
      E. Ovulate bracts as broad as long or broader; east of California.... .... *3. E. Torreyana*
      EE. Ovulate bracts two-thirds as broad as long or less; Death Valley region to Nevada .... *5. E. funerea*
    DD. Seeds more than one-half as wide as long, brown, smooth and almost spherical .... *6. E. californica*
AA. Leaves and bracts of spikes binate, occasionally ternate.
  F. Inner bracts of the ovulate spike membranaceous or herbaceous.
    G. Seeds solitary, or if more than one, light in color.
      H. Seeds almost circular in cross-section.
        I. Seeds smooth, brown to chestnut in color; leaf-bases brown and persistent; stem usually rough .... *7. E. aspera*

II. Seeds furrowed or scabrous, light brown to gray-green; leaf-bases gray and deciduous; stem usually almost smooth.
J. Seeds more than 9 mm. long.................... *8. E. fasciculata*
JJ. Seeds less than 9 mm. long........................ *9. E. Clokeyi*
HH. Seeds trigonal or tetragonal in cross-section.......... *4. E. arenicola*
GG. Seeds paired, brown to almost black.
K. Ovulate spikes sessile or very short-pedunculate; seeds lightly furrowed longitudinally; leaf-bases brown................ *11. E. viridis*
KK. Ovulate spikes usually long-pedunculate; seeds usually smooth; leaf-bases gray or brown.
L. Leaf-bases deciduous and gray; seeds about one-half as thick as long; stem not viscid.
M. Seeds more than 5 mm. in length, slightly exserted, chestnut; bracts with a faint trace of pink.............. *10. E. nevadensis*
MM. Seeds 5 mm. or less in length, almost included, nearly black; bracts bright pink to rose............ *10a. E. nevadensis* f. *rosea*
LL. Leaf-bases persistent and brown; seeds less than one-half as thick as long; stem viscid.............. *12a. E. Coryi* var. *viscida*
FF. Inner bracts of the ovulate spike becoming fleshy; eastern Mexico and United States east of Central New Mexico.
N. Seeds solitary.
O. Seed never less than 6 mm. long, less than 3 mm. broad, slightly exserted.................................... *13. E. antisyphilitica*
OO. Seed less than 6 mm. long, about 3 mm. broad, included.......... .... *13a. E. antisyphilitica* var. *brachycarpa*
NN. Seeds paired.
P. Bracts red; leaf-bases gray and deciduous.
Q. Low compact shrubs, not clambering; ovulate spikes sessile; anthers not known............................ *14. E. compacta*
QQ. Clambering shrubs; ovulate spikes pedunculate; anthers long-stipitate.................................... *15. E. pedunculata*
PP. Bracts yellow to orange; leaf-bases brown and persistent........ .... *12. E. Coryi*

1. **Ephedra trifurca** Torr. ex Wats. in U. S. Geol. Surv. Fortieth Parallel [Bot. King's Exp.] **5**: 329. 1871.

E. occidentalis Torr. in Emory, Mil. Reconn. 151. 1848 [in error, evidently intended for *E. americana* Willd.].

E. trifurcus Torr. in Emory, Mil. Reconn. 152. 1848.

E. antisyphilitica Torr. in Emory, Rep. U. S. Mex. Bound. Surv. **2**: 207. 1859, in part.

E. trifaria Parl. in DC., Prodr. **16**^{2}: 359. 1868.

Erect dioecious shrub, 0.5–2 m. high; branches rigid, hard, terete, up to 3.5 mm. thick, solitary or whorled at the nodes, angle of divergence with the main stem about 30 degrees; inter-

nodes 3–9 cm. long; bark of young stems pale green, almost smooth, with numerous small longitudinal furrows, becoming yellow, then gray-green; bark of older stems cinereous, cracked and somewhat irregularly fissured longitudinally; terminal buds 1 cm. long, spinose; leaves ternately whorled, 5–13 mm. long, subspinosely tipped from a dorso-median thickening, connate for one-half to three-fourths their total length; sheath at first membranaceous, later fibrous, shredded and grayish, persistent; staminate spikes solitary or numerous in a whorl at the nodes of the young branches, obovate, 6–9 mm. long, short-pedunculate, peduncles many-scaled, bracts ternate, in 8–12 whorls, obovate, slightly clawed, 3–4 mm. long, 2–3 mm. broad, membranaceous, reddish-brown, the lower whorls empty; perianth almost equaling the subtending bract; staminal column 4–5 mm. long, one-fourth exserted, with 4–5 short-stipitate anthers; ovulate spikes solitary or numerous in a whorl at the nodes of the young branches, obovate, 10–14 mm. long, short- and scaly-pedunculate or sessile, bracts ternate, in 6–9 whorls, orbicular, clawed, 8–12 mm. long, 9–12 mm. broad, translucent except for the reddish-brown center and basal portion, margins entire; fruit solitary or, occasionally, two or three, usually tetragonal, light brown, smooth, 9–14 mm. long, 1.5–3 mm. wide, equaling the bracts; tubillus straight, conspicuously exserted, the twisted ligulate limb 1 mm. long.

Distribution: southwestern Texas and southern New Mexico to California, and adjacent Mexico.

Specimens examined:

Texas: Limpia Canyon, May 1915, *Allen 177* (G, M); in gravel, semidesert foothills, Franklin Mts., Canutillo, El Paso Co., 3 July 1911, *Barlow* (F); sandy places near El Paso, *Bigelow 3* (G); plain, 3 miles east of Casa Piedra, Presidio Co., 21 Feb. 1937, *Cutler 622* (G, M, P, UW); sands west of gap, Dog Canyon, Santiago Mts., Brewster Co., 27 May 1938, *Cutler 1852–1859* (M); along creek bottom, 3 miles southeast of Castolon, Brewster Co., 29 May 1938, *Cutler 1877, 1879, 1881* (M); sandy plain, 8 miles northwest of Presidio, Presidio Co., 31 May 1938, *Cutler 1920* (M); along dry creek, 17 miles north of Shafter, Presidio Co., 1 June 1938, *Cutler 1942, 1943* (M); along railroad, 2 miles west of Marfa, Presidio Co., 1 June 1938, *Cutler 1952* (M); in sand, forming hummocks, 12 miles northeast of El Paso, El Paso Co., 4 June 1938, *Cutler 1980–1982* (M); flats near Van Horn, 12 May 1901, *Eggert* (M); Mt. Livermore, May 1936, *Hinckley 257* (F); El Paso, 17 April 1884, *Jones 3717* (CA, F, NMAM, P); Marathon, 23 April 1930, *Jones*

26403 (M, P); about 5 miles west of Alpine, Brewster Co., 25 April 1931, *McKelvey 1997, 1998* (P); Boquillas, Brewster Co., 20 July 1937, *Marsh 143* (F); gravelly plain, 3 miles west of Mt. Livermore, Davis Mts., alt. 1800 m., 14 June 1931, *Moore & Steyermark 3083* (CA, G, M); gravelly desert, west side of Chisos Mts., alt. 1065 m., Brewster Co., 27 June 1931, *Moore & Steyermark 3287* (CA, G, M); Hueco Tanks, 1 July 1895, *Mulford 187, 187a* (M); low hills near Fort Davis, 7 July 1917, *Munz 1408* (P); rocky open ground, upper Limpia Canyon, Jeff Davis Co., 17 June 1926, *Palmer 30989* (M); Barstow, 18 April 1902, *Tracy & Earle 66* (F, M); Allamore, 23 April 1932, *Whitehouse 8339* (F).

New Mexico: sandy fields, 7 miles north-northeast of Oro Grand, Otero Co., 4 June 1938, *Cutler 1983, 1984* (M); along creek bed, Rhodes Pass, 30 miles east of Engle, 5 June 1938, *Cutler 2019* (M); fields, 3 miles west of Elephant Butte Dam, Sierra Co., 7 June 1938, *Cutler 2068–2074* (M); on creosote-bush desert near San Marcial, 23 Feb. 1934, *Detwiler 21* (F); near Silver City, 3 April 1919, *Eastwood 8192, 8193* (CA); Nutt, 1420 m., Luna Co., 6 Oct. 1919, *Eggleston 16269* (F); along the Gila River and on the mesa above Cliff, Grant Co., 24 Oct. 1919, *Eggleston 16508* (M); "From the region between the Del Norte and the Gila, and the hills bordering the latter river to the desert west of the Colorado," *Emory Exp.* (type, not seen); wash, 3 miles west of Pyramid Peak, alt. 1200 m., Dona Ana Co., 29 Aug. 1930, *Fosberg S3474* (P); Deming, 11 Aug. 1936, *Gaines* (UNM); Socorro, 1880, *Greene* (F); Lordsburg, 9 April 1930, *Jones 25966* (P); Deming, 9 April 1930, *Jones 26402* (M, P); Organ Mts., Las Cruces, Sept. 1931, *Layton* (I); Mangas Springs, 18 miles northwest of Silver City, Grant Co., 26 Sept. 1903, *Metcalfe 811* (M); hillside near Albuquerque, alt. 1200 m., 17 Dec. 1936, *Miers* (UNM); Deming, 31 Aug. 1895, *Mulford 1025* (I, M); dry rocky hills along the Rio Grande near Caballo Dam, 17 miles east of Hillsboro, Sierra Co., 15 June 1938, *Ownbey & Ownbey 1633* (M); desert plain 8 miles northeast of Lordsburg, Hidalgo Co., 19 June 1938, *Ownbey & Ownbey 1647* (M); Dry Canyon, Sacramento Mts., Alamogordo, alt. 1400 m., 9 April 1902, *Rehn & Viereck* (P, R); San Antonio, 1883, *Rusby* (F); mesa west of Agricultural College, 3 May 1906, *Standley 38* (M); mesa, west of Organ Mts., 22 June 1906, *Standley 441* (M); sandy soil, Valverde, 31 July 1846, *Wislizenus 58* (M); mesa, near Las Cruces, 10 May 1892, *Wooton 426* (NMAM); mesa, near Las Cruces, alt. 1250 m., 5 July 1897, *Wooton 96* (G, M, P); mesa, west of the Organ Mts., Dona Ana Co., 22 April 1899, *Wooton* (NMAM); mesa, west of Organ Mts., Dona Ana Co., alt. 1230 m., 19 April 1905, *Wooton* (I, NMAM); Frontera and Donnana, coll. of 1851–52, *Wright 1884* (G, M).

Arizona: San Bernardino Valley, alt. 1230 m., Cochise Co., 18 April 1928, *Ballou* (CA, P); mesa, north of Rillito Creek, Pima Co., 16 Jan. 1920, *Bartram 16* (P); Yuma, 3 April 1914, *Carlson* (CA); highway 60, near Globe, 1050 m., Gila Co., 21 April 1935, *Collom 341* (M); Yuma, 22 April 1917, *Eastwood 6348* (CA); canyon, Santa Rita Mts., Tucson, 22 March 1919, *Eastwood 8115* (CA); Bowie, 16 May 1919, *Eastwood 8624* (CA); along road from Packard to Payson, 1 Nov. 1928, *Eastwood 16606* (CA); on the road from Prescott to Phoenix, 11 Nov. 1928, *Eastwood 16608* (CA); Sierra Ancha, 7 May 1929, *Eastwood 16950* (CA); Mazatzal Mts., 12 May 1929, *Eastwood 17169* (CA); on road between Globe and Roosevelt, 24 May 1929, *Eastwood 17447* (CA); Pinal Mts., 18 May 1929, *Eastwood 17526* (CA); on road to Rincon Mts., 19 March 1930, *Eastwood 17805, 17811* (CA, G);

Cochise, Feb. 1927, *Ellis & Ledman* (M); on the mesa, north of the Santa Rita Mts., 28 Sept. 1880, *Engelmann* (M); Roadside Mine, Pima Co., 3 April 1932, *Fosberg* (M, P); Douglas, 22 May 1907, *Goodding 2268* (M); desert "prairie," north of Tucson, 4 April 1913, *Greenman & Greenman 74* (M); small range reservation near Tucson, 13 March to 23 April 1903, *Griffiths 3534* (M); Congress Junction, alt. 900 m., 2 May 1903, *Jones* (P); Oracle, alt. 1400 m., 28 Aug. 1903, *Jones* (P); Rodeo, 8 April 1930, *Jones 26400* (M, P); Stein's, 6 May 1930, *Jones 25965* (CA, M, P); Benson, 6 April 1930, *Jones 26401* (P); Sulphur Springs Valley, 18 May 1921, *W. W. Jones 434* (G); mesas, near Tucson, spring 1907, *Lloyd* (F, G); Yuma desert at Monument 204, International Boundary, 17 March 1894, *Mearns 2826* (S); sand dunes, south of Wellton, Gila Desert, Jan. 1916, *Monnet 1110* (CA); rocky washes, 25 miles west of Casa Grande City, 22 March 1935, *Nelson & Nelson 1259* (M, R); sandy Yuma desert near U.S.-Mexican boundary, 26 March 1935, *Nelson & Nelson 1290* (M, R); near Cochise, 24 April 1935, *Nelson & Nelson 1619* (M); Tucson, 2 Feb. 1926, *Nuttall* (CA, F, P); Mohave Agency, 1 April 1876, *Palmer 523½* (G, M); Yuma, 20 March 1881, *Parish & Parish 753* (F, G); Tucson, April 1884, *Parish* (M); Lowell, May 1884, *Parish* (I); Sulphur Springs Valley, 13 April 1894, *Price* (S); mesas, 29 April 1881, *Pringle* (F, G, M); mesa, near Tucson, 2 April 1883, *Pringle* (F); mesa, near Tucson, 21 April 1884, *Pringle* (F); Metcalf, near Clifton, *Reynolds* (CA); wash, west of Desert Lab., Tucson, 22 June 1908, *Sherff* (F); mesas, near Tucson, 8 April 1917, *Shreve 5158* (G); 5 miles west of Rodeo, Cochise Co., 30 April 1933, *Shreve 6282* (F); Gila, June 1852, *Thurber 681* (G); in sand, 7 miles south of Parker on the Bouse road, Yuma Co., 14 April 1922, *Wiegand & Upton 2979* (F); flats of Desert Lab., Tucson, 15 March 1933, *Wiggins 6508* (P); 42 miles northeast of Douglas on road to Rodeo, alt. 1350 m., 7 July 1928, *Wolf 2555* (CA, G, P).

CALIFORNIA: near Salton Sea, 6 March 1922, *Campbell* (CA, P); sand hills, Yuma-El Centro road, Imperial Co., 19 April 1928, *Ferris 7128* (P); Yaqui Well, Colorado Desert, 21 Jan. 1926, *Jones* (P); Imperial Co., near Arizona, 13 March 1920, *Kline* (UW); sand dunes between El Centro, Imperial Co., and Yuma, Arizona, 25 March 1936, *MacFadden 14476* (CA); Laguna Station, 6 May 1894, *Mearns 2937* (S); under overhanging rocks, foot of Mountain Springs Grade, Imperial Co., 23 Feb. 1924, *Munz 7823* (G, P); Colorado desert near Yuma, 27 Dec. 1880, *Parry* (I, M); Agua Caliente, April 1882, *Parry* (M); sand dunes, west of Fort Yuma, Imperial Co., 15 April 1927, *Peirson 7193* (P); sandy soil, Colorado Desert, 12 miles northwest of Westmorland, below sea-level, Imperial Co., 12 March 1931, *Wolf 1870, 1871* (CA).

MEXICO:

COAHUILA: Del Carmen Mts., 29 Aug. 1936, *Marsh 694* (F).

CHIHUAHUA: San Diego, alt. 1830 m., 10 April 1891, *Hartman 642* (G, US); Sierra Madre, 21 June–29 July 1899, *Nelson 6014* (US); vicinity of Chihuahua, about 1300 m., 8–27 April 1908, *Palmer 68* (F, G, M, US); vicinity of Chihuahua, about 1300 m., 1–21 May 1908, *Palmer 172* (US); Chihuahua, 1885, *Pringle 88* (G); mesas, near Chihuahua, 7 April 1886, *Pringle 868* (F, US); mesas, Chihuahua, 20 May 1887, *Pringle 1589* (F); 11 May 1899, *Rose & Hough 4928* (US); Sta. Eulalia plains, 13 April 1885, *Wilkinson 117* (I, US), in part; Sta. Eulalia plains, 2 April 1886, *Wilkinson 120* (I, US).

SONORA: coast of Gulf of California near upper end, 1910, *Lumholtz 24* (G); Colorado River at Colonia Diaz, 24 March 1894, *Mearns 417* (US); Lower Colorado, 1869, *Palmer* (US).

BAJA CALIFORNIA: Gardner's Laguna, 27 April 1894, *Mearns & Schoenfeldt 2916* (S).

E. trifurca is easily recognized by the yellowed and spinosely-tipped branches and the frayed but persistent leaves of the older stems. The species is very constant throughout its entire range.

2. × **Ephedra intermixta** Cutler,[25] n. hyb.
(= Ephedra trifurca × Torreyana).

Erect dioecious shrub, 0.5–1.5 m. high; branches rigid, solid, terete, up to 3.5 mm. thick, solitary or whorled at the nodes, angle of divergence 35–40 degrees; internodes 1–5 cm. long; young stems pale green, smooth and glaucous, with numerous small longitudinal furrows, becoming yellowed; bark cinereous, cracked and fissured; terminal buds spinose to obtuse-conical; leaves ternate, 3–6 mm. long, acutely tipped from a dorso-median thickening, connate for three-fourths their length at first, soon splitting; sheath membranaceous, later fissured; staminate spikes at the nodes of the young branches, ovate, 3–7 mm. long, sessile or short-pedunculate, bracts ternate, in 3–7 whorls, obovate, 2–3 mm. long, 2 mm. broad, mem-

[25] × **Ephedra intermixta** Cutler, hyb. nov.; frutex erectus, dioiceus, 0.5–1.5 m. altus; ramulis rigidis, solidis, teretibus, usque ad 3.5 mm. in diametro, ad nodos solitariis vel verticillatis, angulo declinationis circiter 35–40°; internodiis 1–5 cm. longis; caulibus juventate pallide viridibus, laevibus et glaucis, tenuissime striatis, deinde lutescentibus; rhytidoma cinerea, rimosa, sulcata; gemmis terminalibus pungentibus vel conicis; foliis ternatis, 3–6 mm. longis, ad apicem pungentibus ex dorso-medio crassificatione, primo ad ¾ longitudinis connatis, deinde diffisis; vagina membranacea, deinde corruta; spicis stamineis solitariis vel multis ad nodos ramulorum novorum, ovatis, 3–7 mm. longis, sessilibus vel brevi-pedunculatis, bracteis ternatis, in 3–7 verticillis, obovatis, 2–3 mm. longis, 2 mm. latis, membranaceis, pallide luteis vel pallide fulvis, verticillis inferioribus vacuis; perianthis bracteas subtendentes subaequantibus; columna staminalis 2–5 mm. longa, ½ exserta, 4–7 antheris brevi-stipitatis; spicis femineis solitariis vel multis ad nodos ramulorum novorum, obovatis, 4–7 mm. longis, sessilibus vel brevi-pedunculatis, bracteis ternatis, in verticillis 5–7, suborbicularibus, unguiculatis, marginibus hyalinis, erosis, 4–7 mm. longis, 4–6 mm. latis, membranaceis, pallide luteis; seminibus plerumque solitariis, tri- aut tetragonatis, pallide fulvis, laevibus, 4–6 mm. longis; tubillo recto, multo exserto, limbo ligulato contorto.

branaceous, light yellow to light brown, the lower whorls empty; perianth almost equaling the subtending bract; staminal column 2–5 mm. long, one-half exserted, with 4–7 short-stipitate anthers; ovulate spikes solitary or numerous at the nodes of the young branches, obovate, 4–7 mm. long, sessile or short pedunculate, bracts ternate, in 5–7 whorls, suborbicular, unguiculate, hyaline margins erose, 4–7 mm. long, 4–6 mm. broad, membranaceous, light yellow; seed usually solitary, tri- or tetragonal, light brown, smooth, 4–6 mm. long; tubillus straight, conspicuously exserted, the ligulate limb contorted.

SPECIMENS EXAMINED:

NEW MEXICO: creek bed, Rhodes Pass 30 miles east of Engle, 5 June 1938, *Cutler 2020, 2021* (G, M, US); fields, 3 miles west of Elephant Butte Dam, Sierra Co., 7 June 1938, *Cutler 2075* (G, M TYPE, T, US), *2078* (G, M, T, US).

While making field studies several cases of possible hybridization were observed. Specimens intermediate between *E. trifurca* and *E. Torreyana* were collected both in sandy washes and creek beds, the usual habitat of *E. trifurca,* and in gravelly and sandy fields, the habitat of *E. Torreyana.* The preference of stock for the latter and for *E. intermixta* aids in the field of identification of these two. A comparison with the parent species follows:

E. trifurca	× *E. intermixta*	*E. Torreyana*
Scarcely ever eaten by stock.	Eaten by stock.	Eaten by stock.
Numerous branches at a node.	Numerous to few at a node.	Few branches at a node.
Angle of branch-divergence about 30°.	Angle of branch-divergence about 35–40°.	Angle of branch-divergence about 48°.
Average internode 3.6 cm.	Average internode 2.6 cm.	Average internode 2.4 cm.
Leaves up to 10 mm. long.	Leaves up to 6 mm. long.	Leaves up to 3.5 mm. long.
Bracts usually brown, margins entire.	Bracts from brown and entire to yellow and erose.	Bracts usually yellow, margins erose.
Seeds smooth and light brown.	Seeds smooth and light brown.	Seeds scabrous and light yellow.

3. Ephedra Torreyana Watson in Proc. Am. Acad. **14**: 299. 1879.

E. trifurca Parry in Am. Nat. **9**: 351. 1875.

E. antisyphilitica f. *monstrosa* Torr. ex Stapf in Denkschr. K. Akad. Wiss. Wien **56**²: 43. 1889.

Erect dioecious shrub, 0.25–1 m. high; branches rigid, hard, terete, up to 3.5 mm. thick, solitary or whorled at the nodes, angle of divergence about 48°; internodes 2–5 cm. long; young stems pale blue-green, glaucous, almost smooth with many small longitudinal furrows, becoming gray; bark of older stems cinereous, cracked and irregularly fissured; terminal buds less than 4 mm. long, conical but not spinose; leaves ternately whorled, 2–5 mm. long, obtusely, occasionally acutely, pointed from a brownish-green dorso-median thickening, connate for one- to two-thirds their total length, but later spreading and recurved; sheath at first membranaceous, later fissured, thickened and grayed, subpersistent; staminate spikes solitary to four in a whorl at the nodes of the young branches, ovate, 6–8 mm. long, sessile; bracts ternate, in 6–9 whorls, ovate, slightly clawed, 2–3.5 mm. long, 2-3 mm. broad, membranaceous, cream-coloured to pale yellow, the lower whorls empty; perianth exceeding the subtending bract; staminal column 2.5–4 mm. long, one-fourth to one-half exserted, with 5–8 sessile or short-stipitate anthers; ovulate spikes solitary or several in a whorl at the nodes of the young branches, ovate, 9–13 mm. long, sessile, bracts ternate, in 5–6 whorls, obovate, clawed, 6–9 mm. long, 6–10 mm. broad, hyaline except for the orange-yellow to greenish-yellow center and basal portion, margins minutely toothed, undulate; seed solitary or two, occasionally three, trigonal or tetragonal, light brown to yellow-green, scabrous, 7–10 mm. long, 1.6–3 mm. wide, equaling or slightly exceeding the bracts; tubillus straight, conspicuously exserted, the contorted ligulate limb 1 mm. long.

Distribution: western Colorado to western Texas and westward to northern Arizona and Nevada.

Specimens examined:

Texas: cottonwoods near El Paso, *Bigelow 4* (G, M); 11.15 miles southwest of Big Springs, Howard Co., 18 April 1930 *Cory 2829* (P); dry steep calcium breaks of Palo Duro Canyon, Randall Co., 31 July 1934, *Goodman 2230* (M); dry rocky slopes of Palo Duro Canyon, Randall Co., 3 June 1918, *Palmer 13873* (M, UW); dry rocky slopes, Channing, Hartley Co., 19 June 1918, *Palmer 14165* (M, UW);

Frontera, 1852, *Parry* (M); sandy hills near Frontera, 26 April 1851, ***Wright 1883*** (G TYPE, M) in part.

COLORADO: Deer Run, region of the Gunnison Watershed, alt. 1430 m., 25 Aug. 1901, *Baker 921* (G, M); Grand Junction, May 1892, *Eastwood* (C); Grand Junction, alt. 1370 m., 21 June 1894, *Jones 5468* (F, M, P); Grand Junction, alt. 1350 m., 9 May 1895, *Jones* (P); Grand Junction, alt. 1350 m., 22 May 1895, *Jones* (P); dry hillside, alt. 1760 m., 7 June 1913, *Payson 108* (F, G, M); dry hillside, alt. 1650 m., Naturita, 19 May 1914, *Payson 319* (F, G, I, M); dry rocky hillside, alt. 1650 m., Naturita, 26 May 1914, *Payson 353* (F, G, I, M); shale hills, Ridgeway, 17 June 1924, *Payson & Payson 3833* (G, M); clay to sandy hillside near the Gunnison River, 6 miles west of Delta, Delta Co., 27 Aug. 1937, *Rollins 1975* (G, M).

NEW MEXICO: San Ysidro, 1700 ft., 9 Feb. 1927, *Arsène 19034* (F); Carlsbad, 1 May 1929, *Benke 5022* (F); highlands, Albuquerque, 23 March 1918, *Collins* (G); Pena Blanca, alt. 1600 m., 21 May 1930, *Curtin 108* (F); fields and along railroad tracks, 3 miles north of Escondida, Otero Co., 4 June 1938, *Cutler 1987, 1988, 1990–1997* (M); White Sands, 13 miles w. of Tularosa, Otero Co., 5 June 1938, *Cutler 2004–2015* (M); Jornada del Muerto, 4 miles east of Engle, Sierra Co., 6 June 1938, *Cutler 2049–2053* (M); 7 miles west of Engle, Sierra Co., 7 June 1938, *Cutler 2061, 2062* (M); in fields, 3 miles west of Elephant Butte Dam, Sierra Co., 7 June 1938, *Cutler 2076, 2077, 2079* (M); Farmington, 8 June 1899, *Diehl* (P); on soft "Santa Fe" gravels, San Juan, west side of Rio Grande, Rio Arriba Co., 23 June 1932, *Godwin* (G); Red Valley, on Cuba-San Ysidro road, 7 July 1932, *Goodwin* (G); banks of the Rio Grande River, 19 miles west of Santa Fe, alt. 1650 m., 31 May 1897, *Heller & Heller 3623* (M); Albuquerque, 14 April 1884, *Jones* (P); Rincon, 30 May 1884, *Jones* (P); Organ Pass, 3 May 1930, *Jones* (P); sand dunes west of Alamogordo, 3 May 1930, *Jones 25962, 25964m* (CA, M, P); mesa about two miles east of Albuquerque, alt. 1520 m., 1915, *Kammerer 5* (M); desert hills west of valley, Santa Cruz, Santa Fe Co., 30 June 1936, *Marcelline 1840* (F); sand hills along Cuba Road, near Bloomfield, San Juan Co., 5 July 1929, *Mathias 613, 614* (G, M, P); Santa Fe, June 1874, *Rothrock 80* (F, G); White Sands, Dona Ana Co., 16 July 1897, *Wooton 568* (M); mesa west of the Organ Mts., near Little Mt., Dona Ana Co., 11 May 1902, *Wooton* (NMAM); San Andreas Mts., Jan. 1907, *Wooton* (NMAM); plains 35 miles south of Torrance, alt. 1830 m., 10 Aug. 1909, *Wooton* (NMAM); coll. of 1851-2, *Wright 1882* (M) in part.

ARIZONA: sandy and rocky soil of mesa, Lee's Ferry, 6 July 1927, *Cottam 2611* (BYU); rough hills, Fort Whipple, Sept. 1865, *Coues & Palmer 570* (M); on sands and among flat rocks of mesa 5 miles west of Rock Point, Apache Co., 15 June 1938, *Cutler 2198, 2199* (M); sands, 5 miles south of Dennehotso, Apache Co., 15 June 1938, *Cutler 2211–2213, 2215, 2220* (M); bluffs, edge of Painted Desert, 20 Oct. 1928, *Eastwood 15720* (CA); between Tuba City and Tonalea, Coconino Co., 10 Sept. 1938, *Eastwood & Howell* (CA); Bright Angel Trail, Grand Canyon, 24 May 1903, *Grant* (S); rocky soil near Cameron, alt. 1520 m., 7 June 1922, *Hanson A166* (F, M); Holbrook, May 1900, *Hough* (F, G); Yucca, 13 April 1884, *Jones* (P); Pierce's Ferry, 426 m., 19 April 1894, *Jones 5077az* (P); Bonelli's Ferry, 800 ft., 13 April 1903, *Jones* (P); between Holbrook and Snowflake, 19 May 1931, *McKelvey 2287, 2288* (P); desert plain between Flagstaff and Holbrook, 26 May 1935, *Nelson & Nelson 2136* (M); 12 miles northeast of Tuba City, alt. 1600 m., 3 June 1935, *Peebles & Fulton 11874* (CA); Monument Valley, alt. 1600 m., Navajo Co., 4

June 1935, *Peebles & Fulton 11940* (P); Grand Falls of the Little Colorado River, Coconino Co., *Whiting 756* (UNM); open prairie, Flagstaff road, alt. 1600 m., 5 miles west of Winslow, Coconino Co., 22 May 1922, *Wiegand & Upton 2977* (F).

UTAH: dry hills, Green River, alt. 1380 m., Emery Co., 6 June 1927, *Cottam 2077* (BYU); dry sandy hillside, 10 miles north of Moab, Grand Co., 8 May 1935, *Cottam 6843* (BYU); on sand and gravel, Copper Canyon, 7 miles northwest of Oljato Post, San Juan Co., 16 June 1938, *Cutler 2232, 2245, 2261, 2262* (M); sand flat, San Juan Canyon, 2 miles southwest of Mexican Hat, San Juan Co., 20 June 1938, *Cutler 2320* (M); hills above Comb Wash, 8 miles west of Bluff, San Juan Co., 21 June 1938, *Cutler 2327* (M); 10 miles north of Bluff, San Juan Co., 21 June 1938, *Cutler 2342* (M); Snake Creek, San Juan Co., 15 Sept. 1938, *Eastwood & Howell 6704* (CA); dry hillside, red sandstone ledges, north of St. George, 6 April 1935, *Galway* (BYU); Santa Clara Creek, 20 May 1902, *Goodding 677a* (M); west of Green River, between river and quarry ledge, 20 miles south of Vernal, alt. 1430 m., Uintah Co., 19 June 1931, *Graham 6123* (M); flat above quarry ledge, west side of Green River, 20 miles south of Vernal, alt. 1460 m., 20 June 1931, *Graham 6171* (M); on rocky south slope of Leland Bench, just north of Pariette Creek, alt. 1520 m., Uintah Co., 13 May 1935, *Graham 8840* (F, M); shale breaks, east side of Willow Creek, about 5 miles north of mouth of Agency Draw, alt. 1680 m., Uintah Co., 22 May 1935, *Graham 8933* (M); red hill north of St. George, 8 May 1935, *Hall* (BYU); dry sandy hills, Sugar Loaf Mt., St. George, Washington Co., 15 May 1932, *Harrison 301* (BYU, M); dry sandy wash, Dirty-Devil River canyon, alt. 2115 m., Fruita, Wayne Co., 6 April 1934, *Harrison 7398* (BYU, M); near Lower Crossing, 9 July 1883, *Jones* (P); Green River, 9 May 1890, *Jones* (P); red sand, St. George, alt. 900 m., 26 April 1894, *Jones 5110aq* (P); San Rafael Swell, 28 May 1914, *Jones* (S); southern Utah, 1874, *Parry 250* (G, M); shale outcrops near Willow Creek, 22 miles south of Ouray, Uintah Basin, Uintah Co., alt. 1825 m., 16 June 1937, *Rollins 1719* (G); Granite Creek at foot of the Henry Mts., alt. 1520 m., 5 July 1930, *Stanton 331* (BYU); streamside-washes, Crescent Creek, Henry Mts., alt. 1825 m., 15 July 1930, *Stanton 437* (BYU); slopes and mesas west of St. George, 5 May 1919, *Tidestrom 9300* (G, M).

NEVADA: 5 miles northwest of Las Vegas, 10 May 1938, *Barkley 3232* (M); limestone ledges south of Indian Springs, 1250 m., Clark Co., 12 May 1938, *Clokey 7816* (Clo, M); open hillsides, Dry Lake, 17 April 1905, *Goodding 2234a* (G, M, P); red sand, St. Joe, alt. 425 m., 7 April 1894, *Jones 5029af, 5029ag* (P); Moapa, alt. 425 m., 27 April 1904, *Jones* (P); Amargosa Desert, alt. 1215 m., 27 April 1907, *Jones* (P); Moapa, alt. 517 m., 12 May 1905, *Kennedy* (M); rocky hillside 6 miles north of Alamo, Lincoln Co., 1934, *Maguire, Maguire & Maguire 4715* (M); dry rocky slopes, vicinity public camp, Valley of Fire, Clark Co., 5 April 1934, *Maguire, Maguire & Maguire 4722* (M).

MEXICO:

CHIHUAHUA: near Ojo de Vaca, May 1851, *Thurber 304* (G).

Ephedra Torreyana is not as constant throughout its range as *E. trifurca.* Specimens from St. George, Utah, and to the northwest, differ in having the ovulate bracts brighter yellow, more crenulate and more undulate.

4. × **Ephedra arenicola** Cutler,[26] n. hyb.

(= *Ephedra Torreyana* × *Coryi* var. *viscida* Cutler).

Dioecious shrub, 0.25–1 m. high; branches flexuous, terete, up to 3 mm. thick, opposite or whorled at the nodes, angle of divergence about 35 degrees; internodes 2–5.5 cm. long; young stems green, viscid, slightly rough, with numerous small longitudinal furrows, becoming yellowed; bark cinereous, cracked and fissured; terminal buds subuliform; leaves binate or ternate, 2–6 mm. long, obtusely to setaceously tipped from a dorso-median thickening, connate for two-thirds their length at first, later splitting; staminate specimens not seen; ovulate spikes solitary to many at the nodes of the young branches, peduncles 5–50 mm. long, bracts binate, in 4–6 whorls, slightly unguiculate, narrowly elliptic, 3–8 mm. long, 2–5 mm. broad, membranaceous, margins hyaline and erose; seeds paired, one frequently aborted, scabrous, light brown to light yellow, 4–7 mm. long, almost equaling the bracts; tubillus straight to somewhat curved, slightly exserted, the ligulate limb contorted.

Specimens examined:

Arizona: sands, 5 miles south of Dennehotso, Apache Co., 15 June 1938, *Cutler 2217* (G, M, T, US), *2221* (G, M type, T, US).

Among typical *E. Coryi* var. *viscida* growing upon loose sands was found a hybrid with *E. Torreyana* which grows near by on slightly more stable and rocky areas. A comparison of the hybrid with the parent plants follows:

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[26] × **Ephedra arenicola** Cutler, hyb. nov.; frutex dioiceus, 0.25–1 m. altus; ramulis flexuosis, teretibus, usque ad 3 mm. in diametro, ad nodos oppositis vel verticillatis, angulo declinationis circiter 35°; internodiis 2–5.5 cm. longis; caulibus juventate viridibus, viscidis, parce scabris, tenuissime striatis, deinde lutescentibus; rhytidoma cinerea, rimosa, sulcata; gemmis terminalibus subulatis; foliis binis vel ternatis, 2–6 mm. longis, ad apicem obtusis vel pungentibus ex dorso-medio crassificatione, primo ad ⅔ longitudinis connatis, deinde diffisis; spicis stamineis mihi ignotis; spicis femineis solitariis vel multis ad nodos ramulorum novorum, pedunculis 5–50 mm. longis, bracteis oppositis, in verticillis 4–6, parce unguiculatis, anguste ellipticis, 3–8 mm. longis, 2–5 mm. latis, membranaceis, marginibus hyalinis erosis; seminibus binis, quorum uno saepe abortivo, scabriusculis, pallide fulvis vel pallide luteis, 4–7 mm. longis, bracteas subaequantibus; tubillo recto vel parce curvato, leviter exserto, limbo ligulato contorto.

E. Torreyana	*E. arenicola*	*E. Coryi* var. *viscida*
Average internode 2.4 cm.	Average internode 3.5 cm.	Average internode 3.6 cm.
Angle of branch-divergence about 48°.	Angle of branch-divergence about 35°.	Angle of branch-divergence about 28°.
Stem not viscid.	Stem viscid.	Stem viscid.
Leaves ternate.	Leaves binate and ternate.	Leaves binate.
Leaves short, obtuse, persistent.	Leaves long, setaceous, persistent.	Leaves long, setaceous, deciduous.
Ovulate strobilus sessile.	Ovulate strobilus long-peduncled.	Ovulate strobilus long-peduncled.
Bracts ternate.	Bracts binate.	Bracts binate.
Bracts dry, membranaceous, clawed.	Bracts dry, membranaceous, slightly clawed.	Bracts succulent, connate at base.
Seeds light and scabrous.	Seeds light and scabrous.	Seeds dark and smooth.

5. **Ephedra funerea** Coville & Morton in Jour. Wash. Acad. Sci. **25**: 307. 1935.

Erect dioecious shrub, 0.25–1.5 m. high; branches stiff, hard, terete, up to 3.5 mm. thick, solitary or several, usually three, at the nodes, angle of divergence about 60 degrees; internodes 2–6 cm. long; young stems pale gray-green, glaucous, slightly roughened, glandulose, with many small longitudinal furrows, later gray; bark of older stems cinereous, slightly cracked and fissured; terminal buds 1–4 mm. long, acute-conical, not spinose; leaves ternately whorled, 3–6 mm. long, acutely pointed from a dorso-median thickening, at first connate for one-half to two-thirds their total length, later splitting along the margins and spreading slightly, persistent; staminate spikes one, two or three, at the nodes of the young branches, elongate-elliptic, 5–8 mm. long, sessile or borne on very short scaly-bracted peduncles, bracts ternate, in 6–9 whorls, ovate, short-clawed, 3–4 mm. long, 2–3 mm. broad, membranaceous, yellowish, the lower whorl empty; perianth equaling the subtending bracts; staminal column 3–4 mm. long, one-third exserted, with 4–7 sessile or very short-stipitate anthers; ovulate spikes one, two or three, at the nodes of the young branches, lanceolate-obovate, 8–13 mm. long, on short scaly-bracted peduncles, or sessile, bracts ternate, in 6–9 whorls, elongate-

obovate, broadly clawed, 4–8 mm. long, 3–5 mm. broad, yellow-translucent except for the green thickened central portion, margins slightly dentate; seed solitary, or rarely, two or three, tetragonal, pale green to light brown, smooth to scabrous, 6–9 mm. long, 2–3.5 mm. wide, equaling or barely exceeding the bracts; tubillus straight, exserted, the truncate tip slightly contorted.

Distribution: Death Valley region, California, to Nevada.

SPECIMENS EXAMINED:

CALIFORNIA, DEATH VALLEY REGION: mountain side below Dante's View, 1500 m., 7 April 1935, *Clokey & Templeton 5675, 5676* (Clo, M); Furnace Creek Canyon, alt. 870 m., 16 April 1931, *Coville & Gilman 19* (US); Furnace Creek Canyon, alt. 940 m., 18 April 1931, *Coville & Gilman 108* (US); Boundary Canyon, alt. 1065 m., 24 April 1932, *Coville & Gilman 407–410* (US); Furnace Creek Canyon, near the old town of Ryan, alt. 900 m., 25 April 1932, *Coville & Gilman 444, 445* (US); Furnace Creek Canyon, on the Ryan-Shoshone road, alt. 980 m., 26 April 1932, *Coville & Gilman 447* (US TYPE); Furnace Creek Canyon, junction of the Dante's View road with the Ryan-Shoshone road, alt. 1020 m., 26 April 1932, *Coville & Gilman 448* (US); Warm Springs Canyon, Panamint Mts., about a mile above Warm Springs, alt. 790 m., 30 April 1932, *Coville & Gilman 502, 502A* (US); Furnace Creek Wash, 6 April 1928, *Craig 919* (M); hillside, Ryan, 17–24 March 1924, *Ferris, Scott & Bacigalupi 4036* (S); rocky hillside 1 mile south of Ryan, 16 April 1932, *Hitchcock 12329* (M, P, US); sandy open, 2 miles east of Bradbury Well, Black Mts., 2 April 1928, *Howell 3643* (CA); Funereal Mts., alt. 1200 m., 10 April 1907, *Jones* (P).

NEVADA: gravelly hills, Arden-Mountain Springs, mile 11, alt. 1100 m., Charleston Mts., Clark Co., 22 April 1939, *Clokey 8225* (Clo, M).

6. Ephedra californica Watson in Proc. Am. Acad. **14**: 300. 1879.

Erect or spreading dioecious shrub, 0.3–1 m. high; branches semiflexible to rigid, hard, terete, up to 4 mm. thick, solitary or whorled at the nodes, angle of divergence about 45 degrees; internodes 3–6 cm. long; young stems yellow-green, glaucous, almost smooth, with numerous longitudinal furrows, becoming yellow, then yellow-brown; bark of older stems gray-brown, cracked and irregularly fissured; terminal buds 2–3 mm. long, acute, conical; leaves ternately whorled, 2–6 mm. long, obtusely to acutely tipped from a green-brown dorso-median thickening, connate from one-half to three-fourths their total length; sheath at first membranaceous, later thickened, becoming

brown, hard and fibrous, splitting and recurving, subpersistent; staminate spike solitary or several in a whorl at the nodes of the young branches, ovate, 6–7.5 mm. long, short-pedunculate, peduncles many-scaled, bracts ternate, in 8–12 whorls, ovate, slightly united at the base, 2.5–3 mm. long and broad, membranaceous, light orange-yellow except for the hyaline margins, the lower whorls empty; perianth equaling or slightly exceeding the subtending bract; staminal column 3–5 mm. long, one-third exserted, with 3–7 sessile or short-stipitate anthers; ovulate spikes solitary or several in a whorl at the nodes of the young branches, ovate, 7–10 mm. long, very short- and scaly-pedunculate, bracts ternate, in 4–6 whorls, orbicular, very slightly unguiculate, 5–7 mm. long, 5–10 mm. broad, pale yellow-translucent except for the orange- or green-yellow center and basal portions, margins entire; seed solitary, rarely two, nearly globular but indistinctly tetragonal, light to dark brown or chestnut, smooth, 7–9 mm. in diameter, equaling or slightly exceeding the bracts; tubillus straight, barely exserted, with a short ligulate, scarcely contorted limb.

Distribution: southern California and adjacent Arizona, and northern Baja California.

SPECIMENS EXAMINED:

ARIZONA: Kingman-Yucca road, Mohave Co., 26 March 1927, *Braem* (S).

CALIFORNIA: Palm Springs, Riverside Co., 6 April 1903, *Abrams 3204* (CA, P); hills near Tia Juana, 14 May 1903, *Abrams 3489* (G, M, P, S); dry hillsides near Campo, San Diego Co., 24 May 1903, *Abrams 3600* (G, M, P, S); Jacumba, 31 May 1903, *Abrams 3675* in part (S); Palm Springs, 17 April 1926, *Atsalt* (M); granite soil, Mt. Breckenridge, alt. 900 m., Kern Co., 23 April 1932, *Benson 3358* (S); North Island, 7 May 1904, *Chandler 5165* (S); Coronado, alt. 3 m., near San Diego, June 1893, *Cleveland* (S); mouth of Mosaic Canyon, sea level, Death Valley region, 6 April 1935, *Clokey & Templeton 5784* (Clo, M); field at Coronado, 26 Dec. 1908, *Dudley* (S); Caliente Mts., back of Painted Rock, San Luis Obispo Co., June 1927, *Dudley* (CA); near Ozena P. O., Ventura Co., May 1936, *Dudley* (CA); North Coronado, San Diego Co., 7 April 1913, *Eastwood 2570, 2571* (CA); San Felipe Canyon, Colorado Desert, San Diego Co., 14 April 1913, *Eastwood 2782* (CA); Grapevine Creek, Colorado Desert, San Diego Co., 14 April 1913, *Eastwood 2808* (CA); Tia Juana, San Diego Co., 24 April 1913, *Eastwood 2911* (CA); Palm Springs, San Bernardino Co., 30 April 1913, *Eastwood 3082* (CA); Warren's ranch, Campo, San Diego Co., 22 April 1920, *Eastwood 9412, 9413* (CA); Coalinga, Fresno Co., 31 March 1926, *Eastwood 13453* (CA); near Mountain Spring, San Diego Co., 25 April 1932, *Eastwood 18641* (CA); Morongo Valley, San Bernardino Co., 28

May 1932, *Eastwood 18687* (CA); on road from Barstow to Las Vegas, San Bernardino Co., 30 April 1932, *Eastwood 18766* (CA); on road from Barstow to Las Vegas, San Bernardino Co., 30 April 1932, *Eastwood 18798* (CA); Griswold Creek, southeast of Panoche, San Benito Co., 3 May 1937, *Eastwood & Howell 4273, 4274* (CA); Little Panoche Pass, San Benito Co., 19 April 1938, *Eastwood & Howell 5129, 5130* (CA); Jacumba Springs, San Diego Co., 11–16 April 1924, *Eggleston 19706* (CA, P); sand beach which forms the San Diego Bay, opposite town, 4 Nov. 1880, *Engelmann* (M); Whitewater Desert near San Gorgonio Pass, 10 Nov. 1880, *Engelmann* (M); Whitewater Pass, near Palm Springs, March 1927; *Epling* (M); Box Canyon, San Diego Co., 4 April 1932, *Epling & Robison* (M, CA, S); Cuyama Valley, Kern Co., 13 April 1935, *Esau* (CA); head of Cuyama Valley near Kern Co. line, San Luis Obispo Co., 30 March 1935, *Ferris 9140* (CA, S); in wash near Little Panoche Creek, 25 miles from South Dos Palos on the Panoche road, Fresno Co., 7 April 1938, *Ferris 6953* (P, S); Mohave River bed at Daggett, San Bernardino Co., 14 June 1930, *Ferris 8012* (S); pass in Sheep Hole Mts. between Amboy and Dale P. O., San Bernardino Co., 25 April 1932, *Ferris & Baciga-lupi 8128* (P, S); wash, west end of Sheep Hole Mts., San Bernardino Co., 24 April 1932, *Fosberg 7951* (M); Round Granite Hill near the Narrows, San Diego Co., 14 Nov. 1935, *Gander 2955* (SD); San Luis Rey Valley, near Rancho San Luis Rey, San Diego Co., 21 Jan. 1937, *Gander 3028* (SD); along Coyote Creek, about 3 miles southeast of Lone Palm, north end of Borego Valley, San Diego Co., 6 March 1935, *Gander 13454* (SD); Chuckawalla Peak, Riverside Co., 2 May 1905, *Hall 5979* (S); Palm Springs, Feb. 1926, *Hart* (CA); near Oil City, Kern Co., 22 April 1905, *Heller 7743* (G, M, S); North Island, San Diego Co., July 1902, *Herre* (P); gravelly soil, San Felipe Wash, half way between Borego Valley and Yaqui Well, western Colorado Desert, San Diego Co., 26 Nov. 1927, *Howell 3247* (CA); sandy soil, east end of Morongo Valley, south Mojave Desert, alt. 90 m., San Bernardino Co., 11 March 1928, *Howell 3409* (CA, S); Barstow, Mohave Desert, alt. 700 m., June 1912, *Jepson 4784* (S); San Diego, 16 March 1882, *Jones 3076* (CA, M, P, S); Palm Spring, alt. 61 m., 10 May 1903, *Jones* (CA, P, S); Bakersfield, alt. 305 m., 23 May 1903, *Jones* (P); Funereal Mts., Death Valley, 10 April 1907, *Jones* (P); Barstow, 18 March 1924, *Jones* (S); Old Woman Mts., eastern Mohave Desert, 13 May 1926, *Jones* (P, S); Big Panoche Pass, 12 miles east of Llanada, San Benito Co., 27 Sept. 1932, *Keck 1833* (CA, S); Cuyana Valley, on Ozena road, 3 miles from Santa Maria-Maricopa road, Santa Barbara Co., 6 May 1933, *Keck 2248* (CA, P, S); south of Bakersfield, March 1925, *McCalla* (CA); Morongo Valley, Riverside Co., 20 March 1936, *MacFadden 14475* (CA); Jacumba-Laguna Mts., alt. 760 m., 9 July 1916, *McGregor 138* (S); near Jacumba, 27 June 1925, *McMinn 1431* (S); Jacumba Hot Springs, near Monument No. 233, 29 May 1894, *Mearns 3332* (G, M, S, US); Mountain Springs, 10 May 1894, *Mearns 3024* (S); vicinity of Monument 258 P, International Boundary, 15 July 1894, *Mearns 3923* (S); Jacumba Hot Springs, 24 May 1894, *Mearns & Schoenfeldt 3260* (CA, S, US); dry sandy wash 10 miles west of 29 Palms, alt. 1060 m., 1 May 1921, *Munz 4548* (P); dry slope near Cottonwood Creek and below Barrett Dam, San Diego Co., 10 May 1924, *Munz 8026* (G, P); sandy wash, Sheephole Mts., southern Mohave Desert, alt. 1060 m., 8 April 1935, *Munz 13805* (P, S); sand wash, Mason Valley, eastern San Diego Co., 30 April 1932, *Munz & Hitchcock 12072, 12073* (M, P); dry rocky mesa between Whitewater and Mission Creek, Colorado Desert, 7 May 1922, *Munz &*

Johnston 5286 (P); mountains near Campo, San Diego Co., April 1889, *Orcutt* (M); southwestern part of the Colorado Desert, San Diego Co., April 1889, *Orcutt* (M); Jamul Valley, southern part of San Diego Co., 25 June 1875, *Palmer 364* (Buf, G TYPE, M); San Diego, southern part of San Diego Co., June 1875, *Palmer 365* (Buf, G, M); Whitewater, March 1881, *Parish & Parish 653, 1153* (M, S); Kern River, 1881, *Parry* (M); sandspit opposite San Diego, 17 March 1882, *Parry* (M); San Diego, April 1882, *Parry* (M); Colorado Desert, 6 Dec. 1881, *Pringle* (M); in sand between desert rocks, Mountain Springs, alt. 790 m., San Diego Co., 2 May 1918, *Spencer 807* (CA, G, P); Coronado Beach, San Diego Co., July 1895, *Stokes* (S); Panoche, April 1930, *Van Dyke* (CA); 29 Palms Canyon, Riverside Co., 18 March 1937, *Winblad* (CA); 4½ miles east of Campo, alt. 760 m., on the road to Jacumba, San Diego Co., 27 May 1931, *Wolf 2146* (P, S); Colorado Desert, March 1881, *Wright 188* (G).

BAJA CALIFORNIA: adobe hillside, Refugio Ranch, alt. 620 m., 28 March 1925, *Ballon* (P); near Enseñada, 9 Sept. 1923, *Eastwood 12358* (CA); dunes and sandy slopes, San Quintin, 5 April 1936, *Epling & Stewart* (S); in wash, Santo Tomas Valley at Santo Tomas, 1 March 1934, *Ferris & Bacigalupi 8502* (P, S, US); Jacumba, 2800 ft., 9 July 1922, *Fisher 37* (US); dry hills southwest of Valle Redondo, 30 May 1932, *Fosberg 8381* (M, P, S); San Jose, Tecate, 27 Nov. 1922, *Gallegos 1355* (US); La Huerta at west base of Hanson-Laguna Mts., alt. 850 m., 2 June 1905, *Goldman 1127* (US); Trinidad Valley, northwest base of San Pedro Martir Mts., alt. 820 m., 4 July 1905, *Goldman 1196* (US); San Matias Pass near Diablito Spring, Valle de Trinidad, 26 March 1936, *Harbison 14851* (S); near Santo Tomas, March 1935, *Harvey 535* (US); hills and bluffs near ocean, Enseñada, 7 April 1921, *Johnston 3020* (CA, G, US); Colnet, 15 April 1925, *Jones* (P); San Quintin Bay, 7 June 1925, *Mason 2058, 2059* (CA, US); San Ysidro Ranch, 2 July 1894, *Mearns 3864* (US); about rocks, 50 miles southeast of Tecate, 13 April 1925, *Munz 9567* (P); dry rocky slope 50 miles southeast of Tecate, alt. 1375 m., 13 May 1925, *Munz 9570* (P); Enseñada, 28 Feb. 1906, *Nelson & Goldman 7548* (US); San Selmo, Encinada district, June 1928, *Nutter-Cox* (CA); San Rafael Valley, 18 March 1885, *Orcutt 1271* (C, M); hillside ten miles south of Enseñada, 24 March 1937, *Purer 7127* (M); mountain pass 15 miles south of El Marmol, 2 Feb. 1929, *Reed 6215* (P); wash 2 miles north of Socorro, 4 Feb. 1929, *Reed 6320* (P); San Ysidro, 28 June 1894, *Schoenfeldt 3805* (US); south slope, 8 miles from Rosario on road to El Marmol, 4 March 1930, *Wiggins 4340* (S); in wash, 10 miles from El Marmol, 6 March 1930, *Wiggins 4379* (S); coastal slope 3–4 kilometers north of Enseñada, 12 Sept. 1929, *Wiggins & Gillespie 4016* (CA, G, M, P, S, US); canyon and adjacent slopes, 15–20 miles east of Enseñada on road to Ojos Negros, 14 Sept. 1929, *Wiggins & Gillespie 4062* (CA, S); juniper-covered slopes in vicinity of Ojos Negros, 15 Sept. 1929, *Wiggins & Gillespie 4085* (CA, G, M, P, S, US).

E. californica may be readily distinguished from the other species with ternate leaf arrangement by the browned and thickened leaves of the older stems.

7. **Ephedra aspera** Engelm. ex Wats. in Proc. Am. Acad. **18**: 157. 1883.

E. peninsularis Johnston in Univ. Calif. Pub. Bot. **7**: 437. 1922.

E. Reedii Cory in Rhodora **40**: 216. 1938.

Erect dioecious shrub, 0.25–1.25 m. high; branches rigid, firm, terete, up to 3 mm. thick, opposite or whorled at the nodes, angle of divergence about 35 degrees; internodes 1–5.5 cm. long; young stems pale to dark green, strongly asperous to smooth and glaucous, with numerous small longitudinal furrows, becoming yellow; bark of older stems cinereous, cracked and fissured; terminal buds obtuse-conical; leaves opposite, very rarely ternately whorled, 1–2.5 mm. long, obtusely tipped from a dorso-median thickening, connate for one-half to seven eighths their length; sheath splitting but the parts subpersistent; staminate spikes paired, rarely solitary or whorled, at the nodes of the young branches, obovate, 4–7 mm. long, sessile, or rarely short-pedunculate, bracts opposite, in 6–10 whorls, obovate, 3 mm. long, 2 mm. broad, membranaceous, yellow to red-brown, the lower whorl empty; perianth slightly exceeding the subtending bract; staminal column 4–5 mm. long, one-third exserted, with 4–6 sessile or very short-stipitate anthers; ovulate spikes paired, occasionally solitary, or whorled at the nodes of the young branches, ovate, 6–10 mm. long, sessile or short- and scaly-pedunculate, bracts opposite, in 5–7 whorls, orbicular, 2–5 mm. long, 2–5 mm. broad, thickened, red-brown, margins membranaceous; seed solitary, in cross-section circular to slightly trigonal, with a minute indentation at the tip between the angles, smooth to slightly roughened, light brown to chestnut, 5–8 mm. long, 2.5–4 mm. broad, exceeding by one-third the bracts; tubillus slightly exserted, almost straight, the limb contorted.

Distribution: southwestern United States and northern Mexico.

Specimens examined:

Texas: rocky hills and dry ravines, Frontera, *Bigelow 2* (G); Fort Bliss, 16 June 1917, *Clemens* (CA, P); Marathon, Brewster Co., 20 April 1928, *Cory 920* (G); Brewster Co., 21 April 1928, *Cory 922* (G); Reagan Canyon, Brewster Co., 22 April 1928, *Cory 924* (G); 55.4 miles south of Alpine, Brewster Co., 13 April 1936, *Cory 18547* (G) type of *E. Reedii;* same locality *18548* (TAM); 9 miles north of Sander-

son, Terrell Co., 15 April 1936, *Cory 18736* (G); along railroad, 8 miles west of Sanderson, Terrell Co., 26 May 1938, *Cutler 1846* (M); on talus and summit, Persimmon Gap, Santiago Mts., Brewster Co., 27 May 1938, *Cutler 1851* (M); gravel plain, 8 miles north of Glenn Spring, Brewster Co., 27 May 1938, *Cutler 1863–1868* (M); gravel plain and talus, Fresno Canyon, 25 miles north of Lajitas, Presidio Co., 29 May 1938, *Cutler 1903–1905* (M); gravel plain, 16 miles north of Presidio, Presidio Co., 31 May 1938, *Cutler 1926* (M); slopes and summit, Beach Mts., 8 miles north of Van Horn, Culberson Co., 2–3 June 1938, *Cutler 1958, 1963, 1964, 1966, 1969* (M); canyons near Devil's River, Valverde Co., 13 Sept. 1900, *Eggert* (M); stony hills near Van Horn, 12 May 1901, *Eggert* (M); flats near Van Horn, 12 May 1901, *Eggert* (M); rocky hills near Van Horn, 9 July 1900, *Eggert* (M); alt. 1100 m., southern Brewster Co., 13 July 1927, *Fisher* (P); El Paso, 18 April 1884, *Jones 3726* (CA, F, NMAM, P, S); Indian Hot Springs, 30 April 1930, *Jones 25963* (CA, M, P, S); west of Fort Stockton, 18 April 1931, *Jones 28372* (P); top of Organ Mts., Aug. 1900, *Lemmon 287* (C); Chisos Mts., Aug. 1935, *Marsh 64* (P); Terlingua, Brewster Co., 16 July 1937, *Marsh 103* (F); gravelly mesa north of Chisos Mts., alt. 1065 m., 27 June 1931, *Moore & Steyermark 3258* (CA, G, M, S); Chisos Mts., 28 June 1931, *Mueller 7951* (M); Sierra Blanca, 5 July 1895, *Mulford 272* (M); dry rocky ground near mouth of Pecos River, Valverde Co., 24 April 1928, *Palmer 33475* (M); dry rocky and gravelly ground, plains and foothills of Chisos Mts., 24 May 1928, *Palmer 34145* (M); western Texas, 22 May 1888, *Pringle* (R); vicinity of El Paso, 29 March 1908, *Rose 11634* (G); west base of Lone Mt., Chisos Mts., 21 Feb. 1937, *Sperry 558, 559* (US); El Paso, 188–, *Vasey* (F, I, M); Mt. Franklin, 20 March 1932, *Whitehouse 8340* (CA, F); western Texas, to Frontera, coll. of 1851, *Wright 1883* (M); rocky hills near Frontera, 4 May 1852, *Wright 273?* (G); foothills of Chenate Mts., 9 Sept. 1914, *Young 53* (M).

New Mexico: Pino Blanca, south end of Organ Mts., alt. 1500 m., Dona Ana Co., 11 Sept. 1930, *Fosberg 83960* (P); foot of cliffs near mouth of North Fork, near Three Forks of Rocky Arroyo, Guadalupe Mts., 28 April 1932, *Wilkens 1653* (S); Bishop's Gap, Organ Mts., 4 April 1903, *Wooton* (NMAM).

Arizona: Roosevelt Dam, 17 May 1919, *Eastwood 8676* (CA); Coyote Pass on road from Kingman to Oatman, 16 May 1931, *Eastwood 18425* (CA); Yucca, 14 May 1884, *Jones* (P); near Phoenix, 1880, *Lemmon 252* (G, M); Tucson, 1880, *Lemmon* (M); Coyote Pass, between Kingman and Oatman, 16 May 1931, *McKelvey 2253* (P); Sierra Tucson, 27 May 1884, *Pringle 39* (G); Tempe, 1 April 1894, *Toumey* (S).

California: between Tehachapi and Mojave, 28 June 1908, *Abrams & McGregor 499* (G); eastern base of Coast Range, edge of Colorado Desert, 7 May 1894, *Mearns 2956* (G, M, S); Mountain Springs, San Diego Co., 12 May 1894, *Mearns & Schoenfeldt 3079* (S, US); vicinity of Bonanza King Mine, east slope of Providence Mts., Mojave Desert, alt. 900 m., 21–24 May 1920, *Munz, Johnston & Harwood 4029* (P); Vallecito, June 1882, *Parish & Parish* (M).

Mexico:

tamaulipas: mountains near Miquihuana, alt. 2100–2700 m., 10 June 1898, *Nelson 4472* (F, G, US).

san luis potosi: Sierra de Guascama, Minas de San Rafael, May 1911, *Purpus 5334* (G, M, US).

COAHUILA: dry valley west of Castanuela, 11 April 1847, *Gregg 414* (M); west of Castanuela, 1848–49, *Gregg 53* in part (G); Sierra Madre, 40 miles south of Saltillo, July 1880, *Palmer 1288* (G, M TYPE, US); Saltillo and vicinity, 15–30 April 1898, *Palmer 69* (G, M, UC, US); Sierra de Parras, March 1905, *Purpus 1102* (F, G, M, P); rocky slopes of El Puerto de San Lazaro, San Lazaro, Municipio de Castaños, 17 June 1936, *Wynd & Mueller 143* (M, US).

ZACATECAS: high ridges, Cedros, June 1908, *Kirkwood 24* (F, G); hills, Cedros, June 1908, *Kirkwood & Lloyd 86* (F, M, US).

CHIHUAHUA: Sta. Eulalia Mts., 4 June 1885, *Pringle 38* (G, M, US); Sta. Eulalia plains, 1885, *Wilkinson 118* (F, US).

BAJA CALIFORNIA: Cedros Island, March–June 1897, *Anthony 281* (F, M, S, UC, US); Magdalena Island, 12 Jan. 1889, *Brandegee* (UC), type of *E. peninsularis;* Calamalli, 25 April 1889, *Brandegee* (UC); Cedros Island, 1 April 1897, *Brandegee* (UC); near Canyon Diablo, 20 miles east, 1 May 1933, *Harvey 588* (US); among loose rocks on an old lava flow, Coronados Island, Gulf of California, 18 May 1921, *Johnston 3757* (CA, UC, US); north of Turtle Bay, 2 June 1925, *Mason 1976, 1977* (CA, F, US); Cedros Island, 3 June 1925, *Mason 2021* (US); north end of Cedros Island, 6 June 1925, *Mason 2021a* (CA, US); Cedros Island, 18–20 March 1889, *Palmer 695* (US); Bay of San Bartolome, 27 April 1889, *Pond* (US); rocky soil near Calmalli, alt. 450 m., Jan.–March 1898, *Purpus 6* (F, S, UC, US); Cape region, near Las Animas, Jan.–March 1901, *Purpus 269* (UC); Cedros Island, 11 March 1911, *Rose 16140* (US); San Bartolome Bay, 14 March 1911, *Rose 16236* (US); 20 miles east of Rosario, 8 Feb. 1935, *Shreve 6842* (F).

Although the type description states: "the seed in pairs," all the specimens on the type sheet have the seeds solitary within the strobilus. The strobili, however, are paired at the nodes, and a note on *Palmer 69*, "the female plant has a few very dry seeds attached," indicates that the term "seed" was used for the entire strobilus.

8. **Ephedra fasciculata** A. Nelson in Am. Jour. Bot. **21**: 573. 1935.

Dioecious shrub, often prostrate, 0.25–1 m. high; branches flexuous, solid, terete, up to 3.5 mm. thick, opposite or whorled at the nodes, angle of divergence from the main stem about 35 degrees; internodes 1–5 cm. long; young stems pale green, very slightly asperous to smooth and glaucous, with small longitudinal furrows, becoming yellowed; bark cinereous, cracked and fissured; terminal buds 1–3 mm. long, obtusely conical; leaves opposite, 1–3 mm. long, obtusely tipped from a barely perceptible dorso-median thickening, connate for two-thirds to three-fourths their length at first, later splitting; sheath

hyaline, white, subpersistent; staminate spikes paired or several at the nodes of the young branches, narrowly elliptic, 4–8 mm. long, sessile, bracts opposite, slightly connate, in 4–8 whorls, obovate, 2–3 mm. long, 2 mm. broad, membranaceous, light yellow, the lower whorls empty; perianth exceeding the subtending bract; staminal column 3–9 mm. long, one-fourth to three-fourths exserted, with 6–10 sessile or very short-stipitate anthers; ovulate spikes solitary or several at the nodes of the young branches, elliptic, 6–13 mm. long, sessile or short-pedunculate, bracts opposite, in 4–7 whorls, slightly connate at the base, elliptic, 3–7 mm. long, 2–4 mm. broad, margins hyaline, the back slightly thickened and light brown to green; seed usually solitary, in cross-section almost circular, with numerous longitudinal furrows, light brown, 8–13 mm. long, 3–5 mm. in diameter, one-third to one-half exceeding the bracts; tubillus straight, barely exserted, the ligulate limb bent and slightly contorted.

Distribution: Arizona and southern California.

SPECIMENS EXAMINED:

ARIZONA: Pinal Mts., 18 May 1929, *Eastwood 17314* (CA); Phoenix, alt. 300 m., 6 May 1903, *Jones* (P); Sierra Estrella, 13 April 1931, *Kearney & Peebles 7748, 7759* (P); Tule Tank, Yuma Co., 23 March 1935, *Kearney & Peebles 10897* (P); dry slope, trail from Colorado River to Rampart Cave, Lower Grand Canyon, Mohave Co., 16 June 1937, *Munz 14983* (P); dry sand banks, Phoenix, 2 May 1925, *Nelson 10286* (R TYPE, M, S); rocky slopes, vicinity of Canyon Lake, Apache Trail, 1 May 1935, *Nelson & Nelson 1716* (M).

CALIFORNIA: Kelso, Mohave Desert, alt. 900 m., 2 May 1906, *Jones* (P); canyon near Agua Caliente, April 1882, *Parish & Parish 1238* (G, I, M, S).

9. **Ephedra Clokeyi** Cutler,[27] n. sp.

Erect dioecious shrub, 0.5–1 m. high; branches rigid, solid, terete, up to 3.5 mm. thick, opposite or whorled at the nodes, angle of divergence with the main stem about 40 degrees; inter-

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[27] **Ephedra Clokeyi** Cutler, sp. nov.; frutex erectus, dioiceus, 0.5–1 m. altus; ramulis rigidis, solidis, teretibus, usque ad 3.5 mm. in diametro, ad nodos oppositis vel verticillatis, angulo declinationis circiter 40°; internodiis 2–5 cm. longis; caulibus juventate pallide viridibus, parce scabris vel laevibus et glaucis, tenuissime striatis, deinde lutescentibus; rhytidoma cinerea, rimosa, sulcata; gemmis terminalibus 2–3 mm. longis, obtuso-conicis; foliis oppositis, 1–3 mm. longis, ad

nodes 2–5 cm. long; young stems pale green, slightly asperous to smooth and glaucous, with numerous small longitudinal furrows, becoming yellowed; bark cinereous, cracked and fissured; terminal buds 2–3 mm. long, obtuse-conical; leaves opposite, 1–3 mm. long, obtusely tipped from a dorso-median thickening, connate for one-half to seven eighths their length at first, later split; sheath membranaceous, deciduous; staminate spikes paired or numerous at the nodes of the young branches, obovate, 4–7 mm. long, sessile or very short-pedunculate, bracts opposite, slightly connate, in 5–8 whorls, obovate, 2–3 mm. long, 2 mm. broad, membranaceous, light yellow to light brown, the lower whorls empty; perianth exceeding the subtending bract; staminal column 3–6 mm. long, one-fourth to two-thirds exserted, with 6–9 sessile or very short-stipitate anthers; ovulate spikes paired or numerous at the nodes of the young branches, obovate, 6–10 mm. long, sessile or short-pedunculate, bracts opposite, in 5–8 whorls, slightly connate at the base, broadly elliptic, 3–5 mm. long, 2–4 mm. broad, margins hyaline, the back slightly thickened, light brown to green; seed usually solitary, in cross-section almost circular, with numerous longitudinal furrows, light brown, 5–8 mm. long, 2.8–4 mm. broad; tubillus straight, slightly exserted, the ligulate limb bent and contorted.

Distribution: southern Utah, Arizona, Nevada and southern California.

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apicem obtusis ex dorso-medio crassificatione, primo ad ½–⅞ longitudinis connatis, deinde diffisis; vagina membranacea, decidua; spicis stamineis paribus vel multis ad nodos ramulorum novorum, obovatis, 4–7 mm. longis, sessilibus vel brevi-pedunculatis, bracteis oppositis, parce connatis, in 5–8 verticillis, obovatis, 2–3 mm. longis, 2 mm. latis, membranaceis, pallide luteis vel pallide fulvis, bractearum verticillis inferioribus vacuis; perianthis bracteas subtendentes superantibus; columna staminale 3–6 mm. longa, ¼–⅔ exserta, antheris 6–9 sessilibus vel brevissime stipitatis; spicis femineis paribus vel multis ad nodos ramulorum novorum, obovatis, 6–10 mm. longis, sessilibus vel brevi-pedunculatis, bracteis oppositis, in verticillis 5–8, ad basem parce connatis, late ellipticis, 3–5 mm. longis, 2–4 mm. latis, marginibus hyalinis, dorso parce crassatis, pallide fulvis vel viridibus; seminibus plerumque solitariis, in sectione transverse suborbicularibus, sulcis multis longitudinalibus, pallide fulvis, 5–8 mm. longis, 2.8–4 mm. latis; tubillo recto, leviter exserto, limbo ligulato curvato et contorto.

Specimens examined:

Arizona: canyon above Antler, Mohave Co., 8 April 1928, *Braem* (S); Hermit Trail, Grand Canyon, 9 April 1917, *Eastwood 5965* (CA); Hermit Creek, Grand Canyon, 10 April 1917, *Eastwood 6004a, 6017* (CA); Grand Canyon of the Colorado, 11 April 1917, *Eastwood 6032, 6040* (CA); Hermit Trail, 12 April 1917, *Eastwood 6057* (CA); Bright Angel Trail, Grand Canyon, 14 April 1917, *Eastwood 6100* (CA); Roosevelt Dam, 19 April 1917, *Eastwood 6212* (CA); Hieroglyphic Canyon, Salt River Mts., alt. 500 m., Maricopa Co., 24 March 1932, *Gillespie 5529* (P, S, UC); near Oatman, 23 March 1931, *Harrison & Kearney 7586* (F); Chimehuevis, alt. 1400 m., 21 April 1903, *Jones* (P); Hammock, 17 March 1932, *Jones 29008* (M, P); among the lava rocks, Duncan, 22 March 1930, *Nelson 11280a* (G, S).

Utah: St. George, 2 April 1880, *Jones* (M, S); southern Utah, 1874, *Parry 249* (F, G, I, M); valley of the Virgen near St. George, 1874, *Parry 249* (G); southern Utah, 1874, *Parry 251* in part (G, M).

Nevada: gravel, Mica Spring, alt. 1200 m., 14 April 1894, *Jones 5062* (G, M, P, US); Logan, 5 May 1909, *Kennedy 1841* (I, G, S); rocky slopes of small gully, Frenchman Mt., northeast of Las Vegas, 30 May 1933, *Munz 12955* (P).

California: rocky slope and wash, desert, Cottonwood Springs, Riverside Co., 17 April 1935, *Clokey 6510, 6511, 6512* (Clo, M); among rocks, hillside and wash, desert, Cottonwood Springs, Riverside Co., 17 April 1935, *Clokey 6513* (Clo, M type); rocky slopes and wash in desert, Cottonwood Springs, 17 April 1935, *Clokey 6514* (Clo, M); gravelly hills and ravines, Fort Mojave, 25 Feb. 1861, *Cooper* (M); Box Canyon, San Diego Co., April 1932, *Epling & Robison* (CA, M, S); at bridge in Sentenac Canyon, San Diego Co., 7 March 1935, *Gander 138.12* (SD); Borego Palm Canyon, San Diego Co., 14 April 1936, *Gander 1275* (SD); desert along mountains, alt. 300–770 m., Palm Canyon, Riverside Co., 4 April 1917, *Johnston* (P, S); Imperial Valley, 28 Feb. 1924, *Jones* (P); walls of Box Canyon, western Colorado Desert, eastern San Diego Co., 2 April 1932, *Munz & Hitchcock 12047* (F, M, P); dry rocky slopes, vicinity of Corn Springs, Chuckwalla Mts., Colorado Desert, alt. 460 m., 9–12 April 1922, *Munz & Keck 4789* (P); Mountain Springs, 6 April 1914, *Parish 9070* (S); desert sand, Mountain Springs, San Diego Co., 26 March 1917, *Spencer 206* (G, P); on highway 80, Mountain Springs grade, about 1 mile east of Mountain Springs service station, Imperial Co., western edge of Imperial Valley (Colorado Desert), alt. 250–270 m., 1 May 1938, *Whitaker* (M).

This species has been included under *E. nevadensis* Wats. by most botanists but differs from it in having a solitary seed within the strobilus in contrast to the paired seeds of *E. nevadensis.*

10. Ephedra nevadensis Watson in Proc. Am. Acad. **14**: 298. 1879.

E. antisyphilitica Wats. in U. S. Geol. Surv. Fortieth Parallel [Bot. King's Exp.] **5**: 329, *pl. 39.* 1871, *not* C. A. Mey.

E. antisyphilitica var. *pedunculata* Watson, *loc. cit.*

E. nevadensis Wats. subvar. *paucibracteata* Stapf in Denkschr. K. Akad. Wiss. Wien **56**[2]: 83. 1889.

Erect dioecious shrub, 0.25–1.25 m. high; branches rigid to flexuous, solid, terete, up to 4 mm. thick, opposite or whorled at the nodes, angle of branch-divergence about 45 degrees; internodes 1.5–6 cm. long; young stems pale green, glaucous, almost smooth, with small longitudinal furrows, becoming yellow, then gray; bark cinereous, fissured; leaves binate, rarely ternate, 2–4 mm., rarely to 8 mm. long, obtusely tipped from a dorso-median thickening, connate for one-half to two-thirds their length, later splitting and falling off; staminate spikes solitary to several at the nodes of the young branches, elliptic, 4–8 mm. long, sessile to short-pedunculate, bracts opposite, in 5–9 whorls, obovate, 3–4 mm. long, 2–3 mm. broad, membranaceous, yellow to light brown, the lower whorl empty; perianth slightly exceeding the subtending bracts; staminal column 3–5 mm. long, one-quarter to one-half exserted, with 6–9 sessile to short-stipitate anthers; ovulate spikes solitary to several at the nodes of the young branches, suborbicular, 5–11 mm. long, borne on an almost naked 1–50-mm. long peduncle, bracts binate, in 3–5 whorls, suborbicular, connate at the base, 4–8 mm. long, 3–6 mm. broad, herbaceous, light brown to yellow-green, occasionally tinged with pink; seeds paired, rarely solitary, brown, smooth, 6–9 mm. long, 2–4 mm. broad, equaling or exceeding the bracts; tubillus moderately exserted, slightly recurved, barely contorted.

Distribution: Utah, western Arizona, Nevada, Oregon and California.

Specimens examined:

Arizona: Kingman, 14 April 1931, *Eastwood 18007* (CA); Hackberry, 24 May 1884, *Jones* (P); Camp Lowell, 1880, *Lemmon 251* (G).

Utah: southwest of St. George, alt. 900 m., Washington Co., 3 June 1929, *Cottam 4083* (BYU, P); sandy soil, Santa Clara Bench, alt. 900 m., Washington Co., 24 April 1930, *Cottam 4701* (BYU); dry clay loam, roadside, 6 miles west of Hinckley, alt. 1520 m., Millard Co., 9 May 1935, *Harrison 6305, 6306* (BYU); Santa Clara, 8 April 1880, *Jones* (M); St. George, 2 April 1880, *Jones* (M, S); Frisco, 225 miles southwest of Salt Lake, 22 April 1880, *Jones* (M); Milford, 17 June 1880, *Jones* (P); Milford, 19 June 1880, *Jones* (P); Milford, 22 June 1880, *Jones 1802*

in part (CA); gravel, Marysvale, alt. 1820 m., 4 June 1894, *Jones 5388ag* (CA, P); Dutch Mt., alt. 1620 m., Tooele Co., 15 June 1900, *Jones* (P); Vermilion, 4 June 1901, *Jones* (P); Price Valley, alt. 1520 m., 3 July 1903, *Jones* (P); Leamington, alt. 1520 m., 8 May 1911, *Jones* (CA, S); near Salt Lake, *Macbride* (UI); rocky slopes above public camp, Zion National Park, 2 April 1934, *Maguire, Maguire & Maguire 4723* (M); bluffs near Price, alt. 1800 m., 11 June 1900, *Stokes* (S); slopes and mesas west of St. George, 6 May 1919, *Tidestrom 9303* (M, G, US).

NEVADA: gravelly wash, Kyle Canyon, Charleston Mts., 1350 m., Clark Co., 29 April 1938, *Clokey 7465* (Clo, M); near Pyramid Lake, 24 June 1927, *Eastwood 14734, 14736* (CA, P); sandy deserts near Walker River, 7 June 1859, *Engelmann* (M TYPE of *E. antisyphilitica* var. *pedunculata*, G); Columbus, alt. 1520 m., 20 May 1897, *Jones* (P); Good Springs, 1 May 1905, *Jones* (CA); Big Pine, 3 June 1924, *Jones* (P); Pyramid Lake, Washoe Co., 19 May 1905, *Kennedy 999* (M); Pyramid Lake, alt. 1310 m., 1 June 1913, *Kennedy 1988* (I, M, S); west shore of Pyramid Lake, May 1879, *Lemmon* (G, M); shad-scale desert, 17 miles north of Baker, White Pine Co., 16 June 1933, *Maguire & Becraft 2479* (G, M, P); Atlatl Park, Valley of Fire, Clark Co., 6 April 1934, *Maguire, Maguire & Maguire 4717* (M); in desert pavement, 14 miles north of Glendale, Lincoln Co., 6 April 1934, *Maguire, Maguire & Maguire 4719* (M); Corey Canyon, Wassuk Mts., alt. 1850 m., near Hawthorne, 27 June 1919, *Tidestrom 10099* (M, US); Smoky Valley, alt. 1675 m., July 1868, *Watson 1108* in part (G TYPE).

OREGON: very dry slopes of lower Pueblo Mts., above Catlow's ranch, Harney Co., 4 July 1927, *Henderson 8670* (CA).

CALIFORNIA: desert slopes, Jacumba, San Diego Co., 31 May 1903, *Abrams 3676* (G, M, P); Great Falls Canyon, Argus Mts., Mohave Desert, 18 April 1930, *Bailey & Robison* (CA, M); sandy soil, Walker Pass, Piute Mts., alt. 1200 m., Kern Co., 24 April 1932, *Benson 3446* (S); about 60 miles north of Los Angeles, June 1890, *Coquillett* (M, US); Mojave, Kern Co., 13 May 1913, *Eastwood 3220* (CA); between Jacumba and Mountain Springs, San Diego Co., 24 April 1920, *Eastwood 9522* (CA); between Victorville and Lucerne Valley, San Bernardino Co., 29 April 1932, *Eastwood 18716* (CA); on road to Barstow from Las Vegas, San Bernardino Co., 30 April 1932, *Eastwood 18766, 18791* (CA); Acton, Los Angeles Co., June 1902, *Elmer 3599* (M); Palmdale, 24 April 1926, *Epling* (M); in vacant lot, Lancaster, Los Angeles Co., 12 June 1918, *Ferris 909* (S); low desert hills, on shore of Owen's Lake near Gowan, Inyo Co., 11 July 1918, *Ferris 1347* (S); occasional on rocky slopes, eastern base of Hackberry Mt., near Goffs-Lanfair road, alt. 1100 m., San Bernardino Co., 24 April 1928, *Ferris 7283* (S); yucca-juniper forest, 23 miles west of Lancaster in Antelope Valley, Kern Co., 3 May 1929, *Ferris 7702* (P, S); in yucca grove on Tehachapi road, 6 miles from Mojave, 17–24 March 1924, *Ferris, Scott & Bacigalupi 3874* (S); hills near Victorville, alt. 1050 m., San Bernardino Co., May 1905, *Hall 6212* (S); between Lancaster and Victorville, 27 April 1930, *Hart* (CA); Randsburg, Kern Co., 14 April 1905, *Heller 7703* (M); sandy soil, open desert, Mojave Desert, alt. 900 m., 9 miles southeast of Victorville, San Bernardino Co., 11 June 1927, *Howell 2498* (CA); sandy soil, half way between Victorville and Hesperia, Mojave Desert, alt. 900 m., San Bernardino Co., 12 June 1927, *Howell 2529* (CA); Mohave Desert, near Barstow, alt. 800 m., 8 June 1912, *Jepson 4831* (S); hillside, Victorville, 15 May 1920, *Johnston* (P); in sunny, hot, sandy stretches, Deadman Point, Mohave Desert, alt. 900 m., 10 May 1920, *Johnston* (P);

Bishop, Owen's Valley, alt. 1220 m., 15 May 1897, *Jones* (M, P); Victor, alt. 800 m., 17 May 1903, *Jones* (P); west slope of Walker Pass, alt. 1370 m., Kern Co., 5 May 1932, *Munz 12468* (M, P); Mohave River, southeast California, 1 June 1876, *Palmer 524* (G, M, co-types of *E. nevadensis* subvar. *paucibracteata*); Warren's Well, San Bernardino Mts., alt. 1060 m., 16 June 1894, *Parish 2974* (M); Hesperia, Mojave Desert, 30 May 1918, *Parish 11841* (M, P, S); mountains of the Mojave Desert, March 1882, *Parish & Parish 1368* (M); Cushenberry Springs, Mojave Desert, May 1882, *Parish & Parish 1369* (S); Mojave Desert, May 1882, *Parish & Parish 1369* (G, M); Mohave Desert, 31 May 1882, *Pringle* (M); sandy soil, Argus Mts., alt. 1200–1500 m., April–Sept. 1897, *Purpus 5032* (G, M); Hesperia, April 1892, *Trelease* (M).

The type collection of *E. nevadensis* consists of two species, staminate material of what is now considered *E. nevadensis*, and ovulate material of *E. viridis*. The description by Watson stressed the staminate material and mentioned it first and as Californian specimens of *E. viridis* were cited as being peculiar and perhaps distinct, this is interpreted as leaving the staminate material of Watson's collection as the type. Other material cited in the original description is that of Cooper from Fort Mohave, California (*E. Clokeyi*); of Gregg from northern Mexico (no number is given but this is probably *E. aspera*); and a form from New Mexico with no collector or locality given but probably referring to Wright's or Bigelow's collection of *E. aspera* and stated to differ in having very short peduncles and solitary fruits. The form described as *E. Clokeyi* has been included under *E. nevadensis* by most contemporary botanists but is distinct, having only one seed surrounded by membranaceous bracts as opposed to the paired seeds surrounded by herbaceous bracts in *E. nevadensis*.

This species varies greatly, the southern forms mostly smaller and dark-stemmed; the northern forms with large and almost herbaceous, light-colored stems. The very young shoots are frequently marked by a ternate arrangement of some whorls of leaves.

10a. Ephedra nevadensis forma **rosea** Cutler,[28] n. f.

Differs from the species in having roseate bracts, seeds less than 5.5 mm. long.

[28] **Ephedra nevadensis** forma **rosea** Cutler, f. nov., a specie differt bracteis roseis, seminibus usque ad 5.5 mm. longis.

Distribution: western Nevada and adjacent California.

Specimens examined:

Nevada: near Pyramid Lake, 24 June 1927, *Eastwood 14744* (CA type).

California: Willow Springs, Kern Co., 1 July 1905, *Grinnell 436* (US).

11. Ephedra viridis Coville in Contrib. U. S. Nat. Herb. **4**: 220. 1893.

E. nevadensis var. *viridis* (Coville) Jones in Proc. Calif. Acad. II, **5**: 726. 1895.

E. nevadensis subvar. *pluribracteata* Stapf in Denkschr. K. Akad. Wiss. Wien **56**[2]: 83. 1889.

Erect dioecious shrub, 0.5–1 m. high; branches rigid, firm, terete, up to 3 mm. thick, opposite or numerous at the nodes, angle of divergence about 33 degrees; internodes 1–4.5 cm. long; young stems bright-green to yellow-green, later yellowed; bark of older stems cinereous, cracked and fissured; terminal buds 1–2 mm. long, obtuse-conical; leaves opposite, 1.5–4 mm. long, obtusely to setaceously tipped from a dorso-median thickening, connate for one-third to three-fourths their length, sheath membranaceous-margined, soon falling to leave the thickened and persistent brown base; staminate spikes paired or numerous at the nodes of the young branches, obovate, 5–7 mm. long, sessile, bracts opposite, barely connate at the base, in 6–10 whorls, ovate, 2–4 mm. long, 2–3 mm. broad, membranaceous, light yellow, slightly reddened, the lower whorl empty; perianth slightly exceeding the subtending bract; staminal column 2–4 mm. long, one-fourth to one-half exserted, with 5–8 sessile or almost sessile anthers; ovulate spikes opposite or several at the nodes of the young branches, obovate, 6–10 mm. long, sessile or on short, scaly peduncles, bracts opposite, in 4–8 whorls, ovate, 4–7 mm. long, 2–4 mm. broad; seeds paired, light brown to brown, trigonal, smooth, 5–8 mm. long, usually exceeding the bracts by one-fourth; tubillus straight or slightly bent, exserted, the ligulate limb slightly contorted and meagerly recurved.

Distribution: western Colorado, Utah, western Arizona, Nevada and California.

Specimens examined:

Colorado: slopes, upper juniper area, Uncompahgre Plateau, west of Delta, 6 June 1909, *Tidestrom 2170* (US).

Arizona: below Beaver Dam divide, Mohave Co., 11 May 1938, *Barkley 3333* (M); edge of Walnut Creek, alt. 2000 m., 1 July 1909, *Burrall* (US); near rim of Grand Canyon, east of Point Hope, 3 April 1918, *Collins* (G); dry flats, Lee's Ferry, alt. 1050 m., Coconino Co., 6 July 1927, *Cottam 2610* (BYU); Bright Angel Trail, Grand Canyon, 26–28 Sept. 1913, *Eastwood 3599* (CA); Grand View Trail, Grand Canyon, 16 June 1916, *Eastwood 5715, 5759* (CA); Hermit Trail, Grand Canyon, 18 June 1916, *Eastwood 5872* (CA); Hermit Creek, 10 April 1917, *Eastwood 6026* (CA); trail to Monument Creek, 11 April 1917, *Eastwood 6033, 6042* (CA); Bright Angel Trail, Grand Canyon, 14 April 1917, *Eastwood 6109* (CA); north rim, Grand Canyon, 22 June 1933, *Eastwood & Howell 934* (CA); mesa between Fredonia and Ryan City, alt. 2000 m., Coconino Co., 8 July 1914, *Eggleston 10191* (P); Bright Angel Trail, Grand Canyon, alt. 1220 m., 31 May 1913, *Goldman 2075* (US); Bright Angel Trail, alt. 2080 m., 19 Aug. 1913, *Goldman 2210* (US); near the hotel, Grand Canyon, 25 April 1905, *Goulding* (S); Grand Canyon, 24 May 1903, *Grant 5644* (CA, M, P, S); canyon 2 miles below Pagumpa, alt. 1220 m., 21 April 1894, *Jones 5089r* (P); mesa below Buckskin Mts., alt. 2120 m., 21 Sept. 1894, *Jones 6063q* (P); Chloride, alt. 1370 m., 14 April 1903, *Jones* (P); Chimehuevis, alt. 980 m., 21 April 1903, *Jones* (P); Peach Springs, 14 June 1929, *Jones* (P); Valentine, Mohave Co., 17 April 1934, *Kearney & Peebles 11107* (US); Walnut Canyon, 19 May 1891, *MacDougall 100* (US); near Canyon Diablo, Coconino Co., 18 May 1931, *McKelvey 2285* (P); Bright Angel Trail, Grand Canyon, 6 May 1917, *Meiere* (CA); edge of Walnut Creek, Coconino National Forest and vicinity, 1 July 1929, *Pearson 225* (US); near Flagstaff, June 1900, *Purpus 7087* (US); Holbrook, 6 May 1899, *Zuck* (M, US).

Utah: west ridge of Virgen River, Zion National Park, 9 May 1938, *Barkley 3115* (M); hillsides, Hunt's ranch, alt. 1800 m., Washington Co., 26 Aug. 1927, *Cottam 1189* (BYU); crevices of lava rock, Veyo, alt. 1750 m., Washington Co., 21 June 1928, *Cottam 3368* (BYU); mountain side, alt. 2000 m., Apex Mine, Washington Co., 4 June 1929, *Cottam 4115* (BYU, P); east of Escalante, alt. 1680 m., 18 June 1929, *Cottam 4380* (BYU); cliff, north of Antelope Springs, alt. 2250 m., Millard Co., 19 April 1930, *Cottam 4630* (BYU, M); foot of Lady Mt. Trail, Zion National Park, 19 June 1928, *Craig 1450* (P); among rocks in canyon, 8 miles west of Castle Dale, Emery Co., 25 June 1938, *Cutler 2373–2375* (M); canyon walls, 5 miles west of Elberta, Juab Co., 26 June 1938, *Cutler 2433–2435* (M); foothills 5 miles northeast of Ephraim, alt. 2000 m., San Pete Co., 20–26 May 1914, *Eggleston 10143* (US); Dry Fork Creek, just above Dry Fork town, alt. 2050 m., Uintah Co., 12 May 1935, *Graham 8813* (M); burned-over north slope of Calamity Ridge, south side of White River, 2 miles southeast of mouth of Wolf Creek, alt. 2000 m., 1 June 1935, *Graham 9073* (M, US); Red Wash, just northwest of mouth of Split Mt. Canyon, above Island Park, alt. 1600 m., Uintah Co., 10 June 1935, *Graham 9147* (M, US); on cliff, Cottonwood Creek Canyon, south of Minnie Maud Creek, alt. 1750 m., Carbon Co., 7 July 1935, *Graham 9521* (M, US); Diamond Valley, 22 April 1919, *Hall 527* (US); near Anderson's ranch, Washington Co., 28 July 1927, *Harris N27134* (M); Ephraim Plateau, 4 Aug. 1927, *Harris C27713* (M); rocky cliffs,

Desert Range Experiment Station, alt. 1750 m., Millard Co., 11 May 1935, *Harrison 6382S* (BYU, M); moist north slope, Tintic Mts., east of Eureka, alt. 2120 m., Juab Co., 22 May 1938, *Harrison 8328, 8329* (BYU); rocky sage-brush slope, Ashley Creek Canyon, about 10 miles northwest of Vernal, alt. 1630 m., 14 July 1933, *Hermann 4920* (M); St. George, 2 April 1880, *Jones* (M, P); Frisco, 22 June 1880, *Jones* (CA, M, P); Milford, alt. 1520 m., 22 June 1880, *Jones 1802* (NMAM, S, US); Dutch Mt., 12 June 1891, *Jones* (P); red sand, Belvue, alt. 1100 m., 30 March 1894, *Jones 5001k* (P); gravel, Diamond Valley, alt. 1370 m., 28 April 1894, *Jones 5124* (M, P, US); 10 miles below Kanarra, alt. 1370 m., 12 May 1894, *Jones 5213d* (US); red sand, Johnson, alt. 1600 m., 23 May 1894, *Jones 5289y* (P); red sand, Pahria Canyon, alt. 1600 m., 26 May 1894, *Jones 5297v* (P); gravel, Marvine Laccolite, alt. 1800 m., 23 July 1894, *Jones 5663bf* (P); Monroe, Sevier Co., alt. 1680 m., 24 May 1899, *Jones* (P); Miller Creek, alt. 1800 m., 8 June 1910, *Jones* (P); along Hurricane cliffs, west exposure, 1 mile east of Hurricane, alt. 1020 m., Washington Co., 1 May 1932, *Maguire & Blood 1277* (P); stony ground, Anderson's ranch, St. George, 5 Nov. 1922, *Nelson 9990* (M, R); St. George, collection of 1876, *Parry 251* (G, M, US); Buckskin Mts., Kanab, June 1923, *Rodda* (CA); canyon near Copper Mines, Beaverdam Mts., 6 May 1919, *Tidestrom 9357* (US); dry gumbo hillsides, alt. 1800 m., vicinity of Flaming Gorge, Daggett Co., 31 May 1932, *Williams 463* (CA, P).

Nevada: 6 miles east of Reno, 13 May 1929, *Canby 173* (P); flat, Kyle Canyon, Charleston Mts., alt. 2100 m., Clark Co., 10 May 1936, *Clokey 7027, 7028* (CA, F, M, S, US); slopes, Mt. Wheeler, alt. 2300 m., White Pine Co., 20 June 1928, *Cottam 3300* (BYU); pass north of Olcott Peak, Charleston Mts., alt. 1700 m., Lincoln Co., 6 March 1891, *Coville & Funston 387* (US); Trail Canyon, White Mts., alt. 2400 m., 14 June 1930, *Duran 501* (CA, M, P, S, US, UW); on road from Reno to Pyramid Lake, 24 June 1927, *Eastwood 14719* (CA); Pyramid Lake, June 1927, *Eastwood 14742* (CA); on road to Pyramid Lake from Reno, June 1927, *Eastwood 14761* (CA, P); Victory Highway, 5 miles east of Sparks, 8 June 1933, *Eastwood & Howell 29* (CA); Constantia, Washoe Co., 15 April 1927, *Haley* (CA); hillsides, alt. 2200 m., Deer Lodge, Lincoln Co., 6 June 1935, *Hall* (BYU); Pyramid Lake, 28 May 1916, *Headley 13* (US); Goldfield, alt. 2000 m., 4 June 1912, *Heller 10411* (S, US); Reno, 16 May 1899, *Hillman* (P); dry hills, Hunter's Canyon, vicinity of Reno, alt. 1350–1500 m., 18 July 1913, *Hitchcock 513½* (US); Austin, 16 June 1882, *Jones* (P); Rhyolite, alt. 1160 m., 11 April 1907, *Jones* (M, P); Round Mt., Nye Co., Aug. 1915, *Phares* (S); Carson City, alt. 1400 m., 3 July 1931, *Rose* (CA); dry lakes, Verdi, May–June 1889, *Sonne 491* (M); canyon, Montezuma Mt., west of Goldfield, alt. 2100 m., 4 April 1919, *Tidestrom 9771* (M, US); slopes of Sweetwater Mts., near Sweetwater, alt. 2280 m., 1 July 1919, *Tidestrom 10200* (US); Smoky Valley, alt. 1675 m., July 1868, *Watson 1108* in part (G); hillside between Silver City and Dayton, Lyon Co., 27 July 1933, *Wiggins 6755* (S).

California: rocky hills between Rosamund and Mojave, Kern Co., 30 April 1927, *Abrams 11769* (P, S); west side, Walker Pass, alt. 1130 m., Kern Co., 1 May 1927, *Abrams 11920* (P, S); Sespe Creek, near Ten Sycamore Flat, alt. 700–770 m., Ventura Co., 9 June 1908, *Abrams & McGregor 174* (US); near the Frazier Borax Mine, Mt. Pinos, alt. 1600–1900 m., Ventura Co., 12–14 June 1908, *Abrams & McGregor 217* (S); near Mitchell's Canyon, Providence Mts., Mojave Desert, Nov. 1935, *Alpin* (P); granitic soil, arid ridges about 3 miles west of Benton, Mono Co.,

6 Nov. 1931, *Applegate 6904* (S); 3–5 miles east of Topaz, Mono Co., 20 May 1915, *Bolton* (CA); Santa Inez River, March 1861, *Brewer 347* (M); 3½ miles west of Leevining, alt. 2400 m., Mono Co., 23 Aug. 1933, *Clausen 797* (S); hillside, Cayama Valley, alt. 1500 m., Ventura Co., 22 May 1935, *Clokey 6516* (Clo, M); just above Crystal Spring, Coso Mts., alt. 1840 m., Inyo Co., 12 June 1891, *Coville & Funston 923* (US TYPE); Cuddy Canyon, Mt. Pinos region, 19 June 1896, *Dudley & Lamb 4609* (P); Janesville, 15 July 1935, *Epling & Robison* (M); Lone Pine Trail, above Little Cottonwood Creek, alt. 2900 m., Inyo Co., 23 June 1923, *Ferris 3741* (S); northwestern slope of Maturango Peak, Argus Mts., Inyo Co., 12 April 1930, *Ferris 7857* (S); above old town of Panamint, Surprise Canyon, Panamint Mts., alt. 2250 m., Inyo Co., 12 June 1930, *Ferris 7955* (M, S); open sandy desert, Hackstaff, Lassen Co., *Ferris & Duthie 4* (S); quartzite slope, Gold Mt., above Baldwin Lake, alt. 2200 m., San Bernardino Co., 19 June 1932, *Fosberg 8500* (M); between Susanville and Leavitt Lake, Lassen Co., 12 May 1930, *Gillespie 9347* (S); Mt. Pinos, Ventura Co., 16 May 1923, *Hart* (CA); desert slope, from Big Bear region, San Bernardino Co., 4 July 1924, *Hart 81* (CA); granite sand, mouth of a canyon about three miles south of Bishop, alt. 1380 m., Inyo Co., 21 May 1906, *Heller 8299* (CA, M, S); sandy slopes, Frazier Mt. Park, Pinos region, Kern Co., 25 May 1928, *Howell 3824* (CA); rocky slopes, south side of Surprise Canyon near Panamint City, Panamint Mts., Inyo Co., alt. 2400 m., 14 June 1928, *Howell 3924* (CA); rocky slope, Kern Canyon, 7 miles above Kernville, alt. 830 m., Kern Co., 13 May 1930, *Howell 5028* (CA); Rose Mine, San Bernardino Mts., alt. 2120 m., 2 Sept. 1921, *Jaeger 1061* (P, S); sunny mountain side, Prairie Fork of San Gabriel River, San Antonio Mts., alt. 1530 m., 23 Aug. 1917, *Johnston 1721* (P, S); rocky ground at foot of hill, Deadman Point, alt. 900 m., 16 May 1920, *Johnston* (P); Needles, 7 May 1884; *Jones* (P); Cactus Flat in Cushenbury Canyon, 12 May 1926, *Jones* (P, S); Jacumba, San Diego Co., 30 July 1923, *Kendall* (P); eight miles up Mt. Whitney Trail from Lone Pine, overlooking Lone Pine Creek, alt. 2250 m., Inyo Co., 9 June 1935, *Kimber* (S); Hot Springs Peak, alt. 1460–2120 m., Lassen Co., July 1913, *Monnet 839* (CA); dry loose slope, Big Rock Creek, San Gabriel Mts., alt. 1300 m., Los Angeles Co., 27 May 1923, *Munz 6876* (P); dry banks, Seymour Creek, Mt. Pinos, alt. 1900 m., 10 June 1923, *Munz 6979* (P); dry slope, Baldwin Lake, San Bernardino Mts., alt. 2120 m., 2 June 1924, *Munz 8188* (P); base of cliffs, 5 miles south of Bridgeport, Mono Co., 22 June 1928, *Munz 11082* (P); among rocks, Eagle Mts., Colorado Desert, alt. 250 m., 13 April 1921, *Munz & Keck 4951* (P); near Bishop, Inyo Co., 29 June 1937, *Noldke* (CA); Rock Spring, Mohave Desert, 14 May 1876, *Palmer 525* (M, CO-TYPE of *E. nevadensis* var. *pluribracteata*); Rose Mine, San Bernardino Mts., alt. 1800 m., San Bernardino Co., 17 June 1894, *Parish 297* (M, US); summit of Pilot Knob, Mojave Desert, 14 May 1922, *Pierson & Johnston 6510* (P); sandy soil, Argus Mts., April–Sept. 1897, *Purpus 5312* (M, US); rocky canyon sides, west slope of Pleasant Canyon, Panamint Range, alt. 800 m., Inyo Co., 30 March 1937, *Train* (S); 4–5 miles south of Tehachipi, alt. 1525 m., Kern Co., 17 June 1928, *Wolf 2210* (CA, P, S); rocky soil, Leevining Canyon, Sierra Nevada, alt. 2300 m., Mono Co., 5 Nov. 1931, *Wolf 2551* (S).

The dark and persistent leaf-bases and the sessile or short-pedunculate ovulate strobili readily distinguish this species from *E. nevadensis*. Specimens of *E. viridis* from high alti-

tudes and from the northern portions of the range have darker leaf-bases and more numerous branches but are not sufficiently distinct to separate.

12. Ephedra Coryi Reed in Bull. Torr. Bot. Club **63**: 351, *figs. 1, 2.* 1936.

Erect dioecious shrubs, growing from spreading rhizomes, 0.25–1 m. high; branches terete, up to 2.5 mm. thick, opposite or whorled at the nodes, angle of divergence about 22 degrees; internodes 2–4.5 cm. long; young stems almost herbaceous, bright green, slightly asperous, with numerous small longitudinal furrows, becoming yellow; bark of older stems red-brown, cracked and fissured irregularly; terminal buds 1–3 mm. long, obtusely conical; leaves opposite, acutely tipped from a dorso-median thickening, connate for one-third to three-fourths their length; sheath membranaceous-margined, soon falling to leave the brown, thickened and persistent base; staminate spikes paired or numerous at the nodes of the young branches, obovate, 4–7 mm. long, sessile or short-pedunculate, bracts opposite, slightly connate at the base, in 5–9 whorls, ovate, 2–4 mm. long, 2–3 mm. broad, membranaceous, light yellow, the lower whorl empty; perianth slightly exceeding the subtending bracts; staminal column 2–4 mm. long, one-fourth exserted, with 5–7 sessile or short-stipitate anthers; ovulate spikes opposite or several at the nodes of the young branches, obovate to spherical, 7–15 mm. long, peduncle 3–20 mm. long, with two pairs of bracts, one basal, the other subterminal, bracts opposite, in 3–4 whorls, ovate-acute at first, becoming yellow, fleshy and orbicular at maturity; seeds paired, trigonal, brown to chestnut, smooth, 5–7 mm. long, usually equaling or slightly exceeding the bracts; tubillus straight, slightly exserted, the barely contorted ligulate limb recurved.

Distribution: west-central Texas.

SPECIMENS EXAMINED:

TEXAS: 11¼ miles east of Seminole, Gaines Co., 20 May 1935, *Cory 13711* (US); Boll's ranch, 10 miles southeast of Lubbock, 6 April 1930, *Demaree 7475* (G, M, S); dry prairies near Stanton, Martin Co., 13 June 1900, *Eggert* (M); sandy soil, open ground, Big Spring, Howard Co., 9 July 1917, *Palmer 12491* (CA, M, US); 11¼

miles east of Seminole, Gaines Co., 20 May 1935, *Parks & Cory 11707* (T); Brownfield, *Reed* (US TYPE, not seen); Brownfield, 8 April 1935, *Reed* (TTC); sandy soil, about 12 miles southwest of Lamesa, 22 April 1935, *Reed* (TTC); loose and sandy soil, 1 mile west of Shacktown, 14 June 1934, *Reed 3718* (TTC); sandy, semi-arid soils, level ground, Cedar Lake, about 20 miles southwest of Lamesa, 14 June 1934, *Reed 3719* (TTC); loose and sandy soil, west of Ackerby, 15 June 1934, *Reed 3735* (TTC, US); sandy soil, railroad right-of-way, Meadow, 5 March 1934, *Reed 3897* (TTC); loose sandy soil, between O'Donnell and Lamesa, 16 Sept. 1934, *Reed 4103* (TTC); Meadow, 4 July 1935, *Reed 4200* (TTC); between Wellman and Meadow, 29 July 1934, *Reed 4354* (TTC).

12a. E. Coryi var. viscida Cutler,[29] n. var.

Differs from the species in having the aerial stems frequently branching, the young stems viscid, and the bracts not fleshy.

Distribution: southwestern Colorado, northwestern New Mexico, and adjacent Utah and Arizona.

SPECIMENS EXAMINED:

COLORADO: Deer Run, Gunnison watershed, alt. 1430 m., coll. of 1901, *Baker 921* (P); plains south of Mancos, 8 July 1898, *Baker, Earle & Tracy 397* (M, P); San Juan Valley, July 1875, *Brandegee 7754* (M); dry situations, Church Rock Canyon, 17 June 1927, *Cottam 2319* (BYU); Gunnison Mesa, Grand Junction, 15 May 1916, *Eastwood 5121* (CA); Book Cliff road, Grand Junction, 18 May 1916, *Eastwood 5190, 5191* (CA, S); clay, Grand Junction, alt. 1360 m., 21 June 1894, *Jones 5476v* (P); foothills and mountains, Mesa Co., summer of 1893, *Long* (G); Spruce Canyon, near camp ground, Mesa Verde National Park, 8 July 1929, *Mathias 645* (M, P); dry hills, alt. 1650 m., 28 May 1914, *Payson 367* (M, S); Glenwood Springs, 1 Sept. 1917, *Payson 1199* (M); talus slope of sand and shale, Colorado National Monument, 10 miles southwest of Fruita, alt. 1830 m., 13 Aug. 1937, *Rollins 1931* (CA, M); dry, rocky foothills, Paradox, alt. 1610 m., Montrose Co., 22 June 1912, *Walker 161* (M); dry canyon slope, Norwood Hill, alt. 2200 m., San Miguel Co., 20 Aug. 1912, *Walker 511* (M, P).

NEW MEXICO: Frijoles Canyon, alt. 2000 m., vicinity of Santa Fe, 4 June 1936, *Arséne 22799* (US); along Cuba road, near Bloomfield, San Juan Co., 4 July 1929, *Mathias 611, 612* (M, P); dry hills, alt. 1550–1650 m., vicinity of Farmington, San Juan Co., 17 July 1911, *Standley 6938* (US); mountain side, Bandelier National Monument, 24 June 1935, *Studhalter, Cox & Langford 52449* (US).

ARIZONA: desert near Tuba, 15–31 July 1920, *Clute 100* (M); Montezuma Castle National Monument, Yavapai Co., 20 May 1937, *Cutler 1115* (M, UW); sandy desert, 15 miles east of Tuba City, Coconino Co., 21 May 1937, *Cutler 1147* (M, UW); Monument Canyon, 7 miles southeast of Chinle, Apache Co., 12 June 1938, *Cutler 2143–2148* (M); Canyon de Chelly, near Chinle, Apache Co., 13 June 1938, *Cutler 2156* (M); loose sand, 4 miles south of Round Rock, Apache Co., 14 June

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[29] **E. Coryi** var. **viscida** Cutler, var. nov., a specie differt caulibus ligneis aeriis saepe ramosis, juventate viscidis, bracteis non valde carnosis et non saepe esculentis.

1938, *Cutler 2161–2165, 2169, 2170* (M); sands of mesa, 5 miles west of Rock Point, Apache Co., 15 June 1938, *Cutler 2174, 2183, 2200* (M); loose sand, 10 miles west of Rock Point, 15 June 1938, *Cutler 2209* (M TYPE), *2210* (M); loose sand, 5 miles south of Dennehotso, Apache Co., 15 June 1938, *Cutler 2214, 2216, 2218, 2219* (M); between Tuba City and Tonalea, Coconino Co., 10 Sept. 1938, *Eastwood & Howell* (CA); between Kayenta and Monument Valley, Navajo Co., 14 Sept. 1938, *Eastwood & Howell* (CA); near Canyon Diablo, Coconino Co., 18 May 1931, *McKelvey 2284* (P); steep, rocky, brushy slopes near Indian Gardens, Oak Creek Canyon, 23 May 1935, *Nelson & Nelson 2087* (M); near Ganado, 17 May 1934, *Peebles 9352* (US); sandstone bluff, edge of marsh, alt. 1520 m., near Tuba City, Navajo Co., 2 June 1935, *Peebles & Fulton 11857* (US); 14 miles north of Kayenta, alt. 1600 m., Navajo Co., 4 June 1935, *Peebles & Fulton 11935* (US); gorge of the Little Colorado River, alt. 1650 m., Coconino Co., 8 June 1937, *Peebles & Smith 13340* (US); in sand, 5 miles southeast of Tuba City, alt. 1550 m., Coconino Co., 8 June 1937, *Peebles & Smith 13361* (US); Oraibi, alt. 2000 m., 29 June 1935, *Whiting 756/732* (UNM); Navajo Springs, 24 July 1892, *Wooton* (NNAM).

UTAH: cliffs, Moab, 7 June 1927, *Cottam 2138* (BYU); sandy bluff, alt. 1800 m., Blanding, San Juan Co., 1 July 1927, *Cottam 2502, 2518* (BYU); dry flat, Monument Valley, alt. 1680 m., 2 July 1927, *Cottam 2566* (BYU); hills above Comb Wash, 8 miles west of Bluff, San Juan Co., 21 June 1936, *Cutler 2328* (M); loose sand, 4 miles north of Bluff, San Juan Co., 21 June 1938, *Cutler 2340, 2341* (M); 6 miles northwest of La Sal Junction, San Juan Co., 23 June 1938, *Cutler 2365* (M); under an overhanging cliff of Augusta Natural Bridge, San Juan Co., 7 May 1933, *Harrison 5913* (M); canyon bottom, Augusta Natural Bridge, San Juan Co., 7 May 1933, *Harrison 5914* (M); Moab, 30 Aug. 1891, *Jones* (P); 1½ miles east of Armstrong Canyon, National Bridges Monument, alt. 1750 m., San Juan Co., 22 June 1932, *Maguire & Redd 1631* (M); western slope of La Sal Mts., near Little Springs, alt. 2000–2200 m., 5–6 July 1911, *Rydberg & Garrett 8571* (US).

This variety is dominant over extensive stretches of sandy desert in the Navajo Indian Reservation and near-by regions and forms large hummocks. In the north and at high altitudes it is difficult to distinguish vegetative material from *E. viridis*, but the long peduncle of the ovulate strobili and the usual viscid stems distinguish other specimens. A probable hybrid of this variety and *E. Torreyana* has been given the binomial *Ephedra arenicola* earlier in this paper.

13. Ephedra antisyphilitica Berland. ex C. A. Mey. in Mém. Acad. Imp. Sci. St. Petersburg, VI, Sci. Nat. **5**: 291. 1846.

E. occidentalis Torr. ex Parl. in DC., Prodr. **16**²: 354. 1868.

E. texana Reed in Bull. Torr. Bot. Club **62**: 43. 1935.

Erect or spreading dioecious shrub, 0.25–1 m. high; branches stiff, hard, terete, up to 4 mm. thick, alternate or whorled at the nodes, angle of divergence about 48 degrees; internodes 2–5

cm. long; young stems green, glaucous, almost smooth, with many small longitudinal furrows, becoming yellow-green, then gray-green; bark of older stems cinereous, slightly cracked and fissured; terminal buds 2–3 mm. long, obtusely pointed; leaves binate, 1–3 mm. long, obtusely tipped from a dorso-median herbaceous thickening, connate for two-thirds to nine-tenths their total length; sheath membranaceous, later splitting and falling; staminate spikes solitary or paired at the nodes of the young branches, lanceolate-elliptic, 5–8 mm. long, almost sessile, 5–8 pairs of bracts, obovate, one-eighth connate at the base, 2–3.5 mm. long, 2–3 mm. broad, slightly thickened, margins membranaceous, pale green to reddish, the lower pair empty; perianth slightly exceeding the subtending bract; staminal column 4–5 mm. long, one-half exserted, with 4–6 sessile or very short-stipitate anthers; ovulate spikes solitary or paired at the nodes of the young branches, rarely several at a node, elliptic, 6–11 mm. long, nearly sessile, 4–6 pairs of bracts, ovate, one-eighth to seven-eighths connate, the inner pairs becoming fleshy, red, succulent when ripe; seed solitary, trigonal or occasionally tetragonal, light brown to chestnut, smooth, 6–9 mm. long, 2–3.5 mm. broad, conspicuously exserted; tubillus straight, slightly exserted, ligulate limb slightly contorted.

Distribution: southwestern Oklahoma, and west-central Texas to northeastern Mexico.

Specimens examined:

Oklahoma: along the Red River, Harman Co., 16 Dec. 1933, *Goodman & Barkley* (F, G, M).

Texas: desert plains, Nolan Co., 3 Aug. 1934, *Barkley* (M); Rio Frio, "entre Laredo et Dejar," Feb. 1828, *Berlandier 1590* [=*320*] (C, M, co-types); Big Springs, 20–23 May 1899, *Bray 394* (US); San Antonio, Bexar Co., 15 April 1911, *Clemens & Clemens 380* (CA, M, P); 9 miles northwest of Edinburg, Hidalgo Co., 30 Dec. 1933, *Clover 1593* (CA); 3 miles east of San Angelo, Tom Green Co., 28 April 1931, *Cory* (M); 15 miles north of Eldorado, Schleicher Co., 29 April 1931, *Cory* (US); Croton Camp, Matador Ranch, Dickens Co., 15 June 1904, *Coville 1871* (US); Texas Agricultural Experiment Station number 14, west of Rock Springs, Edwards Co., 24 May 1938, *Cutler 1815, 1816* (M); pasture 12 miles south of Sonora, Sutton Co., 24 May 1938, *Cutler 1817* (M); ungrazed field, 10 miles south of Sonora, Sutton Co., 24 May 1938, *Cutler 1819, 1820* (M); 12 miles southwest of Sonora, Sutton Co., 24 May 1938, *Cutler 1822* (M); 14 miles south of Juno, Val Verde Co., 24 May 1938, *Cutler 1830* (M); pastures, 7 miles west of Comstock,

Val Verde Co., 24 May 1938, *Cutler 1831* (M); along railroad 4 miles w. of Shumla, Val Verde Co., 24 May 1938, *Cutler 1833* (M); pasture ½ mile west of Dryden, Terrell Co., 24 May 1938, *Cutler 1837–1839* (M); gravel plain 1 mile west of Sanderson, Terrell Co., 26 May 1938, *Cutler 1840–1842* (M); along railroad 8 miles west of Sanderson, Terrell Co., 26 May 1938, *Cutler 1845* (M); rocky hills near Stanton, Martin Co., 13 June 1900, *Eggert* (M); hills and valleys, Laredo, 18 Feb. 1919, *Hanson 344* (G, M, UW); Nibo Mt., Gillespie Co., *Jermy 154* (M, US); Experiment Station, Sonora, 21 April 1931, *Jones 28371* (CA, M, P, S); Laredo, 24 March 1932, *Jones 29009* (M); below Laredo, 26 March 1932, *Jones* (P); between Uvalde and Del Rio, 18 April 1931, *McKelvey 1895* (P); between the Frio and the Nueces rivers, on the road to Laredo, 27–28 Jan. 1880, *Palmer 1289, 1292* (M); dry limestone hills, Concan, Uvalde Co., 14 June 1916, *Palmer 10190* (US, S); dry limestone hills, San Angelo, Tom Green Co., 28 June 1916, *Palmer 10309* (M, S, US); dry calcareous hillsides, Telegraph, Kimble Co., 8 Oct. 1916, *Palmer 10951* (M, US); sandstone hills, Campbelton, Atascosa Co., 9 March 1917, *Palmer 11238* (CA, M, UC, US); dry rocky hills, Brownwood, Brown Co., 18 Oct. 1917, *Palmer 13028* (CA, M, US); dry limestone ledges near Brownwood, Brown Co., 31 Oct. 1924, *Palmer 26783* (M); along caprock escarpment and the broken country to the eastward, Buffalo Springs, Lubbock, 15 April 1934, *Reed 3628* (US); caliche soil along escarpment, Buffalo Springs, Lubbock, *Reed 3946* (R); Buffalo Springs, Lubbock, 30 Sept. 1934, *Reed 4113* (R); Johnson's ranch, Yellow House Canyon, Lubbock, 2 March 1935, *Reed 4143* (R); Rocky Bluffs, Brown Co., April 1882, *Reverchon 925* (F, M, US); vicinity of Langtry, 27 March 1908, *Rose 11621* (US); pasture, La Salle Co., 4 May 1919, *Schulz 90* (US); near Paint Rock, Concho Co., 27 April 1931, *Terry V21* (P); near Eagle Pass, Maverick Co., 6 Aug. 1925, *Tharp 3334* (US); San Antonio, *Wilkinson 113* (M).

MEXICO:

SAN LUIS POTOSI: region of San Luis Potosi, 1878, *Parry & Palmer 854* (M).

NUEVO LEON: mountains near Icamole, 3 Feb. 1907, *Safford 1251* (M).

Ephedra antisyphilitica and *E. pedunculata* have been regarded frequently as a single species, yet they are very distinct and no true intergrading forms have been found. The former species rarely has a pair of seeds but never assumes the clambering habit or attains the long stipitation of the anthers that characterizes *E. pedunculata.* The latter appears frequently to have a habit of erect growth when it has been repeatedly grazed over by stock.

13a. E. antisyphilitica var. **brachycarpa** Cory in Rhodora **40:** 218. 1938.

Like the species except the ovulate spikes are shorter, less than 6 mm. long, and broader; seed broader, about 3 mm. wide, definitely trigonous, included.

Distribution: known only from Kent and Bexar counties, Texas.

SPECIMENS EXAMINED:
TEXAS: eastern Bexar Co., 25 March 1935, *Parks 12175* (US TYPE, not seen); eastern Bexar Co., 25 March 1935, *Parks, 12176, 12177* (T).

14. Ephedra compacta Rose in Contrib. U. S. Nat. Herb. **12**: 261. 1909.

Erect or spreading, compact dioecious shrub, 0.3–0.5 m. high; branches stiff, hard, almost terete, up to 2.5 mm. thick, opposite or whorled at the nodes, angle of divergence about 37°; internodes 0.5–3 cm. long; young stems gray-green, glaucous, with several longitudinal furrows, becoming distinctly gray; bark of older stems gray-brown, lightly fissured and cracked; terminal buds about 1.5 mm. long, conical; leaves opposite, 1.5–3 mm. long, obtusely pointed, connate for one-half to seven-eighths their length; sheath chartaceous, red-brown in earlier stages, later gray and divided, subpersistent; staminate spikes not seen; ovulate spikes solitary or paired at the nodes of the young branches, ovate, 4–8 mm. long, almost sessile, 3–5 pairs bracts, broadly ovate, 4–5 mm. long, 3–5 mm. broad, one-eighth to three-fourths connate when mature, the inner pairs red and succulent; seeds paired, light brown to chestnut, almost smooth, 3.5–5.5 mm. long, 2–3 mm. broad, slightly exceeding the bracts; tubillus straight, barely exserted, the tip truncate.

Distribution: east-central Mexico, Coahuila to Oaxaca.

SPECIMENS EXAMINED:
MEXICO:
OAXACA: Las Naranjas, Aug. 1908, *Purpus 3054* (F, M, US).
PUEBLA: Esperanza, Sept. 1911, *Purpus 5698* (F, M, US); near Tehuacan, 1–2 Aug. 1901, *Rose & Hay 5835* (US); near El Riego, Tehuacan, 2 Sept. 1905, *Rose & Hay 10023* (US); hills west of town, near Tehuacan, 2 Sept. 1906, *Rose & Rose 11274* (US TYPE); near Tehuacan, 30 Aug.–8 Sept. 1905, *Rose, Painter & Rose 10023* (US).
SAN LUIS POTOSI: Charcas, July–Aug. 1934, *Lundell 5165* (CA, F, US).
COAHUILA: rocky soil, battlefield near Buena Vista, 19 May 1848, *Gregg 53* in part (G, M).

15. Ephedra pedunculata Engelm. ex Wats. in Proc. Am. Acad. **18**: 157. 1883.

Vine-like shrub, trailing on ground or clambering over bushes and trees, often to a height of 6–7 m., dioecious; branches lax, firm, terete, up to 3 mm. thick, alternate, or rarely, whorled at the nodes, angle of divergence about 52 degrees, internodes 1–7 cm. long; young stems gray-green, glaucous, almost smooth, with several moderately deep longitudinal furrows, becoming more green, then yellow-green; bark of older stems cinereous, slightly cracked and fissured; terminal buds 1–3 mm. long, attenuated; leaves binate, 1–3 mm. long, obtusely tipped from a dorso-median herbaceous thickening, connate from two-thirds to nine-tenths their total length; sheath membranaceous, later splitting; staminate spikes solitary or paired at the nodes of the young branches, lanceolate-elliptic, 4–8 mm. long, peduncles 0–12 mm. long, 6–12 pairs of bracts, obovate, free or one-eighth connate at the base, 1.5–3.5 mm. long, 1.5–3 mm. broad, slightly thickened, margins membranaceous, pale yellow to reddish, the lower pair empty; perianth slightly exceeding the subtending bract; staminal column 3–5 mm. long, one-half exserted, with 4–6 definitely stipitate anthers; ovulate spikes solitary or paired at the nodes of the young branches, rarely several at a node, elliptic, 6–10 mm. long, peduncles 1–20 mm. long, 3–6 pairs of bracts, ovate, one-eighth to seven-eighths connate, the inner pairs becoming fleshy, red, succulent when ripe; seeds paired, trigonal, light-brown to chestnut, smooth, 4–9 mm. long, 2–3.5 mm. broad, conspicuously exserted; tubillus slightly kinked, somewhat exserted, limb contorted.

Distribution: southwestern Texas east of the Pecos River, to San Luis Potosi, Mexico.

SPECIMENS EXAMINED:

TEXAS: between Barrocetes ranch and Aquilares, Zapata Co., 19 Dec. 1933, *Clover 1584* (CA); Ranch Experiment Station, Edwards Co., 9 Sept. 1931, *Cory* (M); climbing on fence and on spiny shrubs, 12 miles south-southwest of Sonora, Sutton Co., 24 May 1938, *Cutler 1821* (M); climbing over trees and shrubs, 14 miles south of Juno, Val Verde Co., 24 May 1938, *Cutler 1827* (M); 1890, *Nealley 258* (F, R); Uvalde, 90 miles northwest of San Antonio, 1880, *Palmer 1291* (M TYPE, US); Rio Frio, Oct. 1851, *Parry* (M); Barrens, Brown Co., April 1882, *Reverchon* (F); Uvalde Co., June 1846, *Reverchon 1658* (M).

MEXICO:

TAMAULIPAS: La Sardiña, Sierra de San Carlos, alt. 650 m., 14 Aug. 1930, *Bartlett 1095* (US).

SAN LUIS POTOSI: en route from San Luis Potosi to Tampico, Dec. 1878–Feb. 1879, *Palmer* (I); San Luis Potosi and vicinity, July–Aug. 1898, *Palmer 702* (US); San Luis Potosi, 1878, *Parry & Palmer 855* (F, I, M, US); San Luis Potosi, Aug. 1879, *Schaffner 279* (CA, F, P, US).

NUEVO LEON: Lampazos, 26 June, *Edwards* (F).

COAHUILA: States of Coahuila and Nuevo Leon, July 1880, *Palmer 1289* (I, M, US); Juarez, 100 miles north of Monclova, Sept. 1880, *Palmer 1290* (I, M, US); Saltillo, 1898, *Palmer 283* (F, M, US).

ZACATECAS: plains, Cedros, June 1908, *Lloyd 75, 214* (M, US); near Concepcion del Oro, 22 Nov. 1902, *Palmer 372* (US).

CHIHUAHUA: Bachimba Canyon, 15 April 1885, *Pringle 134* (F, US); Sta. Eulalia plains, 13 April 1885, *Wilkinson 117* (US) in part.

DURANGO: dry valley between Mapimi and Guajuguilla, 18 April 1867, *Gregg 484* (M); Durango, April–Nov. 1896, *Palmer 149* (F, M, US).

List of Exsiccatae

The distribution numbers are in *italics*. Unnumbered collections are indicated by a dash. The numbers in parentheses are the species numbers used in this monograph.

Abrams, Le Roy. *3204, 3489, 3600, 3676* in part (6); *3676* in part (10); *11769, 11920* (11).
Abrams, L. R., & E. A. McGregor. *499* (7); *174, 217* (11).
Allen, Eva. *177* (1).
Anthony, A. W. *281* (7).
Aplin, J. A. — (11).
Applegate, E. I. *6904* (11).
Arséne, Bro. G. *19034* (3); *22799* (12a).
Atsalt, S. (6).
Bacigalupi, Rimo, see—R. S. Ferris.
Bailey, Harold, & W. Robison. — (10).
Baker, Carl F. *921* in part (6); *921* in part (12a).
Baker, C. F., F. S. Earle, & S. M. Tracy. *397* (12a).
Ballon, L. — (6).
Ballou, F. O. — (1).
Barkley, Fred A. *3232* (3); *3115, 3333* (11); — (13); see—G. J. Goodman.
Barlow, Bronson. — (1).
Bartlett, Harley Harris. *1095* (15).
Bartram, Edwin B. *16* (1).
Becraft, R. J., see—B. Maguire.
Benke, *5022* (3).
Benson, Lyman. *3358* (6); *3446* (10).
Berlandier, J. L. [*320*] *1590* (13).
Bigelow, J. M. *3* (1); *4* (3); *2* (7).
Blood, H. L., see—B. Maguire.
Bolton, A. L. — (11).
Braem, Selma. — (6); — (9).
Bray, William. *394* (13).
Brandegee, T. S. — (7); *7754* (12a).
Brewer, William H. *347* (11).
Burrall, H. D. — (11).
Campbell, Mrs. R. W. — (1).
Canby, W. *173* (11).
Carlson, John I. — (1).
Chandler, H. P. *5165* (6).
Clausen, J. *797* (11).
Clemens, Mr. & Mrs. Joseph. *380* (13).
Clemens, Mrs. Joseph. — (7).
Cleveland, D. — (6).
Clokey, Ira W. *7816* (3); *8225* (5); *6510-6514* (9); *7465* (10); *6516, 7127, 7027, 7028* (11).
Clokey, I. W., & Bonnie C. Templeton. *5675, 5676* (5); *5784* (6).

Clover, Elzada U. *1593* (13); *1584* (15).
Clute, Willard N. *100* (12a).
Collins, John Franklin. — (3); — (11).
Collom, Mrs. Rose E. *341* (1).
Cooper, Juan. — (9).
Coquillett, D. W. — (10).
Cory, Victor L. *2829* (3); *920, 922, 924, 18547, 18548, 18736* (7); *13711* (12); — (13); — (15); see—H. B. Parks.
Cottam, W. P. *2077, 2611, 6843* (3); *4083, 4701* (10); *1189, 2610, 3300, 3368, 4115, 4380, 4630* (11); *2138, 2319, 2502, 2518, 2566* (12a).
Coues, Elliott, & Edward Palmer. *570* (3).
Coville, Frederick Vernon. *1871* (13).
Coville, F. V., & F. Funston. *387, 923* (11).
Coville, F. V., & M. F. Gilman. *19, 108, 407–410, 444, 445, 447, 448, 502, 502a* (5).
Cox, M., see—R. A. Studhalter.
Craig, T. *919* (5); *1450* (11).
Curtin. — *108* (3).
Cutler, Hugh Carson. *622, 1852-1859, 1877, 1879, 1881, 1920, 1942, 1943, 1952, 1980-1984, 2019, 2068-2074* (1); *2020, 2021, 2075, 2078* (2); *1987, 1988, 1990-1997, 2004-2015, 2049-2053, 2061-2062, 2076, 2077, 2079, 2198, 2199, 2211-2213, 2215, 2220, 2232, 2245, 2261, 2262, 2320, 2327, 2342,* (3); *2217, 2221* (4); *1846, 1851, 1863-1868, 1903-1905, 1926, 1958, 1963, 1964, 1966, 1969* (7); *2373-2375, 2433-2435* (11); *1115, 1147, 2143-2148, 2156, 2161-2165, 2169, 2170, 2174, 2183, 2200, 2209, 2210, 2214, 2216, 2218, 2219, 2328, 2340, 2341, 2365* (12a); *1815-1817, 1819, 1820, 1822, 1830, 1831, 1833, 1837-1839, 1840-1842, 1845* (13); *1821, 1827* (15).
Demaree, Delsie. *7475* (12).
Detwiler, S. B. *21* (1).
Diehl, I. E. — (3).
Dudley, W. R. — (6).
Dudley, W. R., & F. H. Lamb. *4609* (11).
Duran, Victor. *501* (11).
Duthie, R., see—R. S. Ferris.
Earle, F. S. see—C. F. Baker; see—S. M. Tracy.
Eastwood, Alice. *6348, 8115, 8192, 8193, 8624, 16608, 16808, 16950, 17169, 17447, 17526, 17805, 17811* (1); *15720,* — (3); *2570, 2571, 2782, 2808, 2911, 3082, 9412, 9413, 12358, 13453, 18641, 18687, 18766, 18798* (6); *8676, 18425* (7); *17314* (8); *5965, 6004a, 6017, 6032, 6040, 6057, 6100, 6212* (9); *3220, 9522, 14734, 14736, 18007, 18716, 18768, 18791* (10); *14744* (10a); *3599, 5715, 5759, 5872, 6026, 6033, 6042, 6109, 14719, 14742, 14761* (11); *5121, 5190, 5191* (12a).
Eastwood, A., & J. T. Howell. *6704,* — (3); *4273, 4274, 5129, 5130* (6); *29, 934* (11); — (12a).
Edwards, Mary T. — (15).
Eggert, Henry. — (1); — (7); — (12); — (13).
Eggleston, Willard W. *16269, 16508* (1); *19706* (6); *10143, 10191* (11).
Ellis, J. H., & O. S. Ledman. — (1).
Elmer, A. D. E. *3599* (10).
Engelmann, George. — (1); — (6).
Engelmann, Henry. — (10).
Epling, Carl Clawson. — (6); — (10).
Epling, C. C., & W. Robison. — (6); — (9); — (11).
Epling, C. C., & W. Stewart. — (6).
Esau, Katherine. — (6).
Ferris, Roxana S. *7128* (1); *6953, 8012, 9140* (6); *909, 1347, 7283, 7702* (10); *3741, 7857, 7955* (11).
Ferris, R. S., & R. Bacigalupi. *8128* (6); *8502* (6).
Ferris, R. S., & R. Duthie. *4* (11).
Ferris, R. S., F. M. Scott, & R. Bacigalupi. *4036* (5); *3874* (10).
Fisher, George L. *37* (6); — (7).
Fosberg, F. R. *S3474,* — (1); *7951, 8381* (6); *S3960* (7); *8500* (11).

Fulton, H. J., see—R. H. Peebles.
Funston, F., see—F. V. Coville.
Gaines, G. W. — (1).
Gallegos, J. M. *1355* (6).
Galway, D. H. — (3).
Gander, Frank F. *2955, 3028, 13454* (6); *138.12, 1275* (9).
Garrett, A. O., see—P. A. Rydberg.
Gillespie, D. K. *9347* (11); see—I. L. Wiggins.
Gillespie, J. W. *5529* (9).
Gilman, M. F., see—F. V. Coville.
Godwin, A. — (3).
Goldman, E. A. *1127, 1196* (6); *2075, 2210* (11); see—E. W. Nelson.
Goodding, Leslie N. *2268* (1); *677a, 2234a* (3).
Goodman, George Jones. *2230, 2234a* (3).
Goodman, G. J., & F. A. Barkley. — (13).
Goodwin, R. — (3).
Goulding, J. M. — (11).
Graham, Edward H. *6123, 6171, 8840, 8933* (3); *8813, 9073, 9147, 9521* (11).
Grant, George B. — (3); *5644* (11).
Greene, Edward L. — (1).
Greenman, Jesse More, Jr. & Milton Turner. *74* (1).
Gregg, Josiah. *53* in part, *414* (7); *53* in part (14); *484* (15).
Griffiths, David. *3534* (1).
Grinnell, Fordyce. *436* (10a).
Haley, G. — (11).
Hall, D.— (3); — (11).
Hall, H. M. *5979* (6); *6212* (10); *527* (11).
Hanson, Herbert C. *A166* (3); *344* (13).
Harbison, C. F. *14851* (6).
Harris, J. Arthur. *M27134, C27713* (11).
Harrison, B. F. *301, 7398* (3); *6305, 6306* (10); *6382S, 8328, 8329* (11); *5913, 5914* (12a); see—W. D. Stanton.
Harrison, J. G., & T. H. Kearney. *7586* (9).
Hart, Cecil. — (6); — (10); *81* — (11).
Hartman, C. V. *642* (1).
Harvey, Mrs. D. R. *535* (6); *588* (7).
Harwood, R. D., see—P. A. Munz.
Hay, R., see—J. N. Rose.
Headley, F. B. *13* (11).
Heller, A. Arthur. *7743* (6); *7703* (10); *8299, 10411* (11).
Heller, A. A., & E. Gertrude. *3623* (3).
Henderson, L. F. *8670* (10).
Hermann, F. J. *4920* (11).
Herre, A. C. — (6).
Hillmann, P. H. — (11).
Hinckley, L. C. *257* (1).
Hitchcock, Albert S. *513 1/2* (11).
Hitchcock, C. Leo. *12329* (5); see—P. A. Munz.
Hough, W., see—J. W. Rose.
Hough, Mrs. W. — (3).
Howell, John Thomas. *3643* (5); *3247, 3409* (6); *2498, 2529* (10); *3824, 3924, 5028* (11); see—A. Eastwood.
Jaeger, E. C. *1061* (11).
Jepson, Willis L. *4784* (6); *4831* (10).
Jermy, C. *154* (13).
Johnston, Ivan M. *3020* (6); *3757* (7); — (9); — (10); *1721*, — (11); see—P. A. Munz; see—R. H. Peebles.
Jones, Marcus E. *3717, 25965, 25966, 26400, 26401, 26402, 26403*, — (1); *5029af, 5029ag, 5077az, 5110aq, 5468, 25962, 25964m*, — (3); — (5); *3076*, — (6); *3726, 25963, 28372*, — (7); — (8); *5062, 29008*, — (9); *1802* in part, *5388ag*, — (10); *1802* in part, *5001k, 5089r, 5124, 5213d, 5289y, 5297v, 5663bf, 6063c*, — (11); *5476v*, — (12a); *28371, 29009*, — (13).
Jones, W. W. *434* (1).
Kammerer, Alfred L. *5* (3).
Kearney, T. H., see—J. G. Harrison.
Kearney, T. H., & R. H. Peebles, *7748, 7759, 10897* (8); *11107* (11).

Keck, David D. *1833, 2248* (6); see—P. A. Munz.
Kellogg, N. B. — (3).
Kendall, L. — (11).
Kennedy, P. B. — (3); *1841* (9); *999, 1988* (10).
Kimber, G. C. — (11).
Kirkwood, J. E. *24* (7).
Kirkwood, J. E., & F. E. Lloyd. *86* (7).
Kline, E. — (1).
Lamb, F. H., see—W. R. Dudley.
Langford, M., see—R. A. Studhalter.
Layton, D. V. — (1).
Ledman, O. S., see—J. H. Ellis.
Lemmon, J. G. *252, 287,* — (7); *251,* — (10).
Lindheimer, Ferdinand. *414* in part (15).
Lloyd, F. E. — (1); *75, 214* (15); see—J. E. Kirkwood.
Long, H. C. — (12a).
Lumholtz, Carl. *24* (1).
Lundell, C. L. *5165* (14).
Macbride, Thomas H. — (10).
McCalla, W. C. — (6).
MacDougall, Douglas T. *100* (11).
MacFadden, F. A. *14476* (1); *14475* (6).
McGregor, E. A. *138* (6); see—L. R. Abrams.
McKelvey, Susan Delano. *1997, 1998* (1); *2287, 2288* (3); *2253* (7); *2285* (11); *2284* (12a); *1895* (13).
McMinn, H. E. *1431* (6).
Maguire, Bassett, & R. J. Becraft. *2479* (10).
Maguire, B., & H. L. Blood. *1277* (11).
Maguire, B., R. & G. B. *4715, 4722* (3); *4723, 4717, 4719* (10).
Maguire, B., & J. D. Redd. *1631* (12a).
Marcelline, Sister M. *1840* (3).
Marsh, Ernest G. *143, 694* (1); *64, 103* (7).
Mason, H. L. *2058, 2059* (6); *1976, 1977, 2021, 2021a* (7).
Mathias, Mildred E. *613, 614* (3); *611, 612, 645* (12a).
Mearns, Edgar A. *417, 2826, 2937* (1); *3024, 3332, 3864, 3923* (6); *2956* (7).
Mearns, E. A., & L. Schoenfeldt. *2916* (1); *3260* (6); *3079* (7).
Meiere, Mrs. Ernest. — (11).
Metcalfe, O. B. *811* (1).
Miers, S. M. — (1).
Monnet, P. *1110* (1); *839* (11).
Moore, John Adam, & Julian A. Steyermark. *3083, 3287* (1); *3258* (7).
Mueller, C. H. *7951* (7); see—F. L. Wynd.
Mulford, A. Isabel. *187, 187a, 1025* (1); *272* (7).
Munz, Philip A. *1408, 7823* (1); *4548, 8026, 9567, 9570, 13805* (6); *14983* (8); *12955* (9); *12468* (10); *6876, 6979, 8188, 11082* (11).
Munz, P. A., & C. L. Hitchcock. *12072, 12073* (6); *12047* (9).
Munz, P. A., & I. M. Johnston. *5286* (6).
Munz, P. A., I. M. Johnston & R. D. Harwood. *4029* (7).
Munz, P. A., & D. D. Keck. *4789* (9); *4951* (11).
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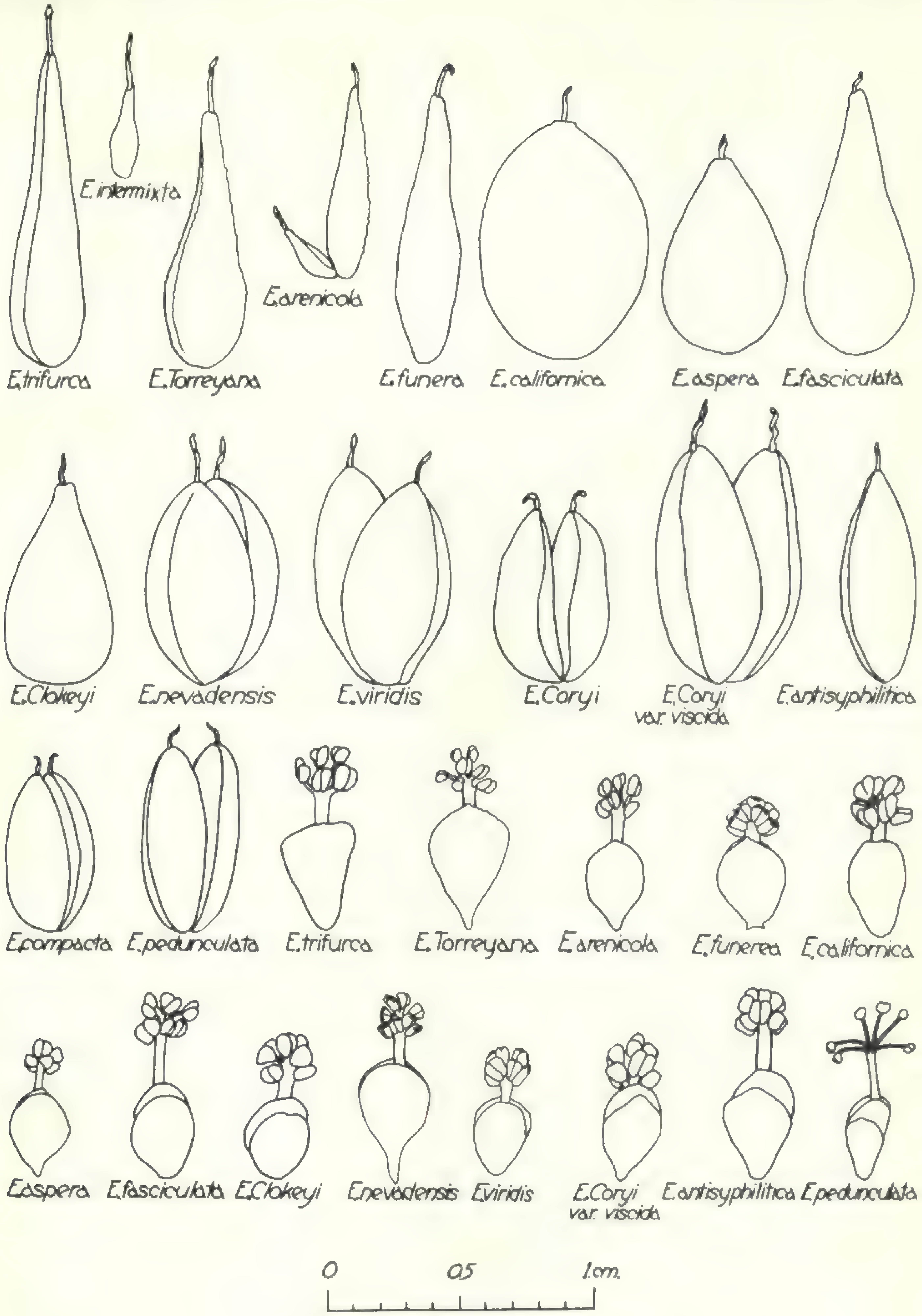
Explanation of Plate

PLATE 27

Typical seeds with tubilli; typical staminate bracts with included perianths and antherophores.



CUTLER—MONOGRAPH OF EPHEDRA

Explanation of Plate

PLATE 28

Geographical distribution of species of *Ephedra*.

Fig. 1. *E. trifurca* ————————
E. intermixta ●
E. Torreyana — — - - - - - - —
E. arenicola ×
E. funerea ————————*
E. californica —||—||—||—

Fig. 2. *E. aspera* ————————
E. fasciculata . . . .
E. Clokeyi — — — — —

Fig. 3. *E. nevadensis* — - - — — — —*
E. viridis ————————
E. Coryi —×—×—×—
E. Coryi var. *viscida* —||—||—||—

Fig. 4. *E. antisyphilitica* ————————
E. compacta —||—||—||—
E. pedunculata — — — — —

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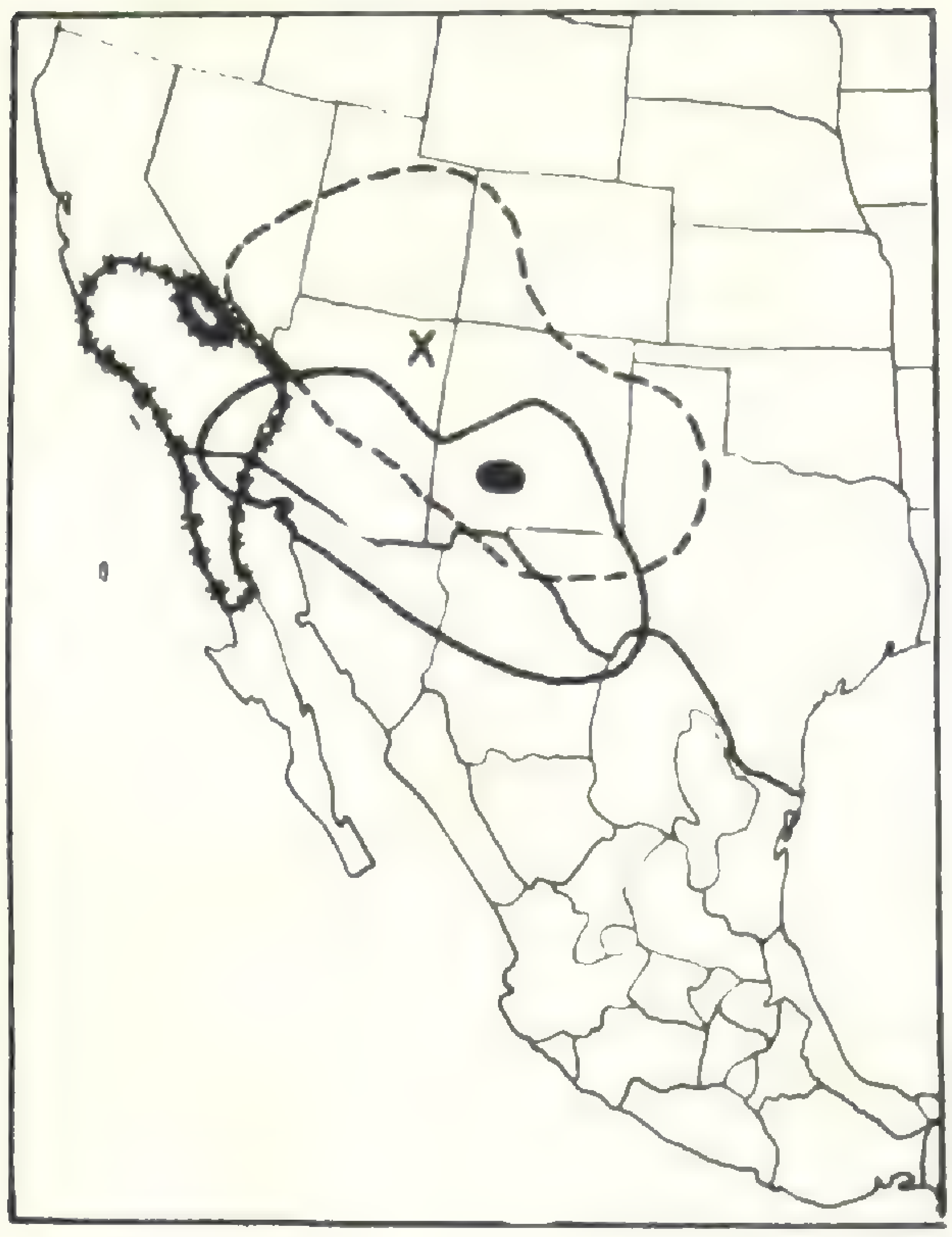
* Note: Since the maps were made *E. funerea* has been collected in southeastern Nevada (Clark Co.), and *E. nevadensis*, in Harney Co., Oregon.



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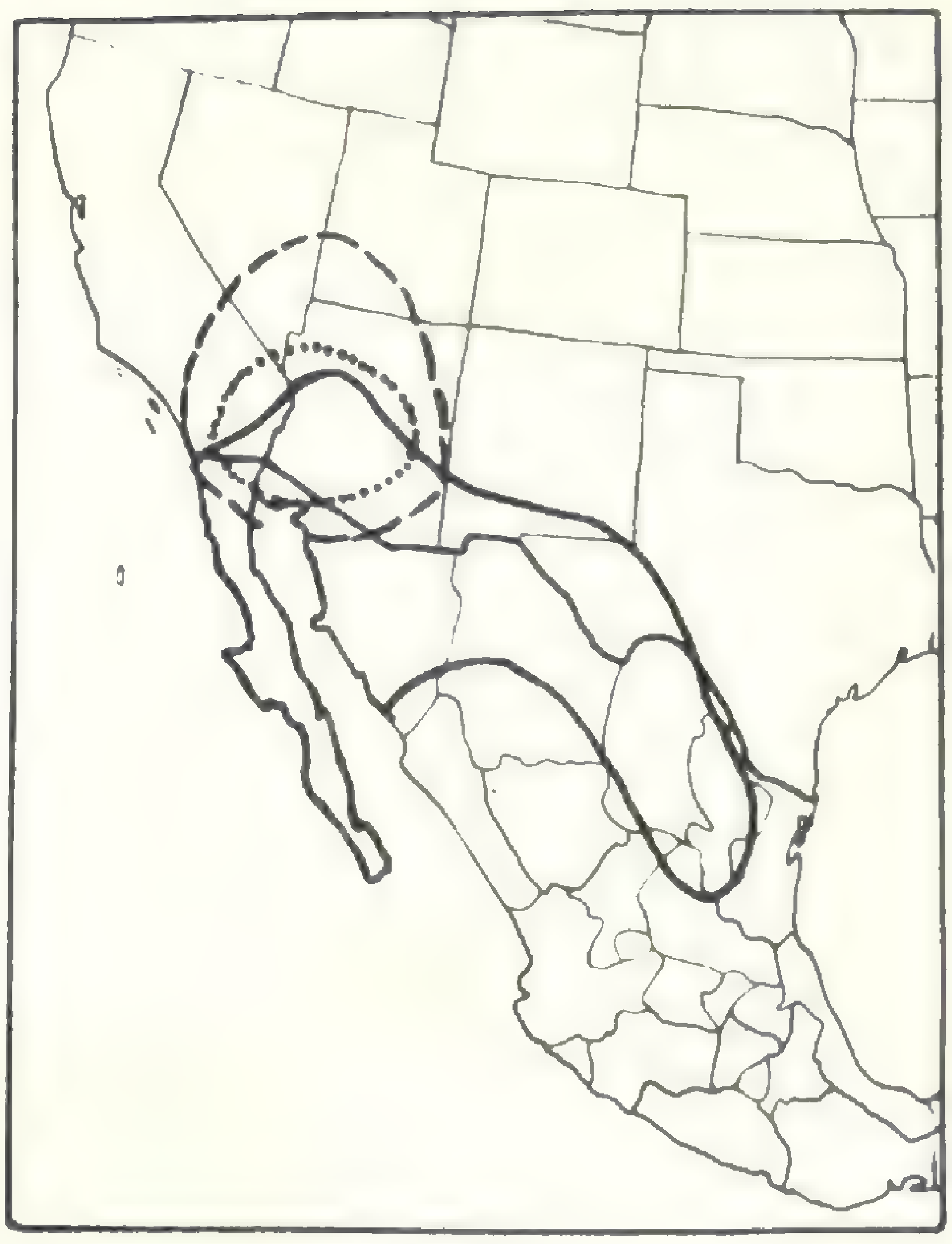

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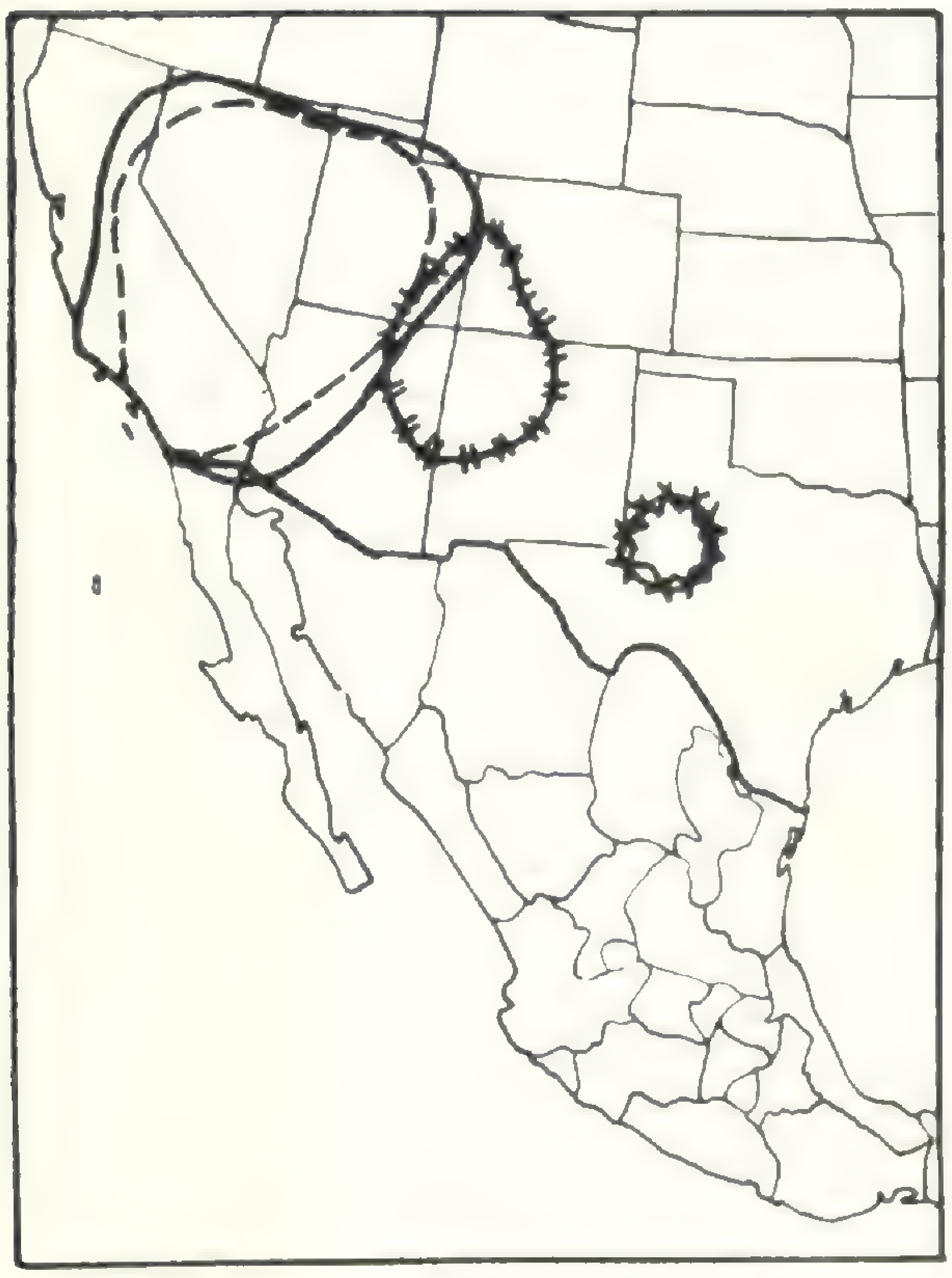

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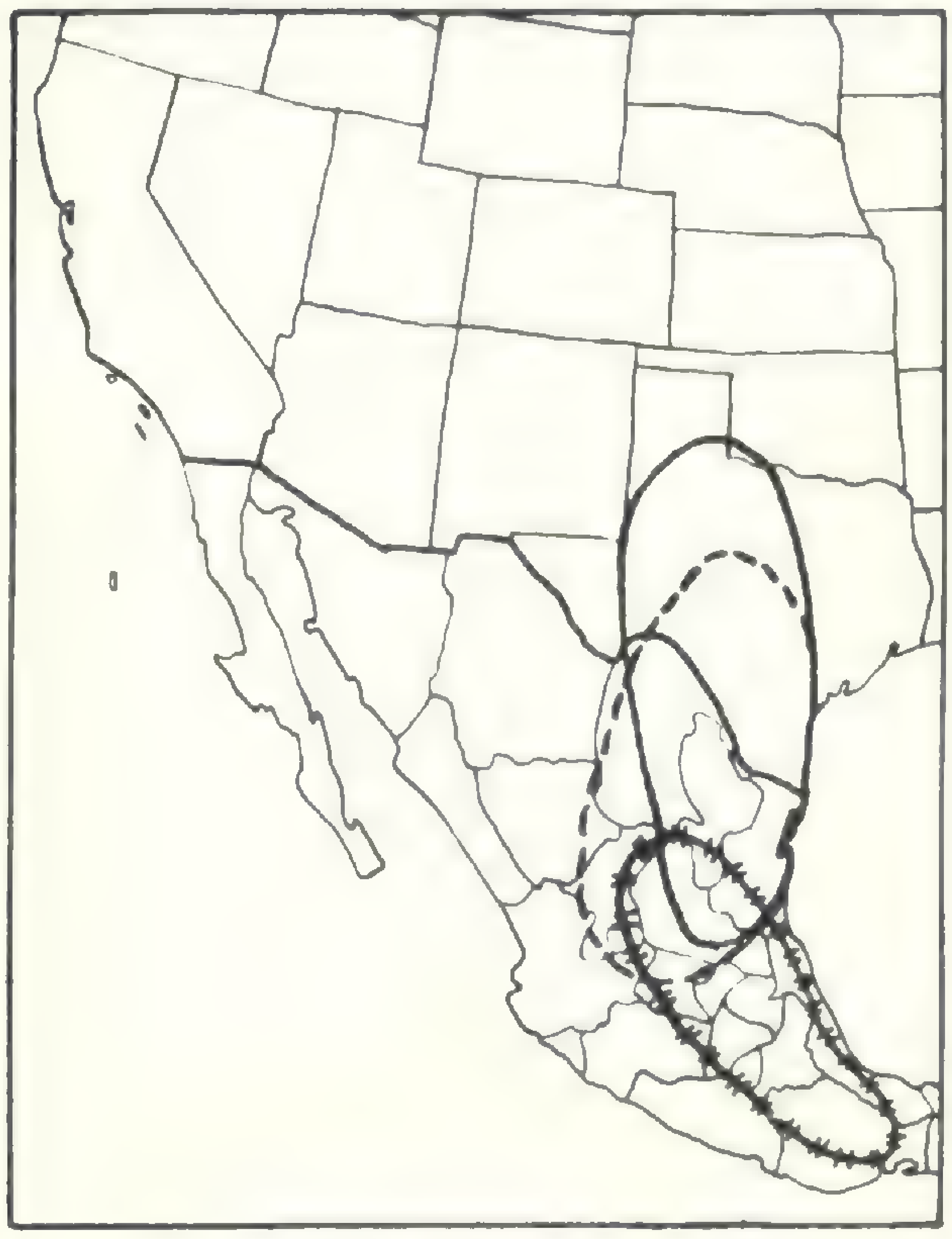

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